

INFLORESCENCE ARCHITECTURE AND EVOLUTION
IN THE FAGACEAE

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INFLORESCENCE ARCHITECTURE is receiving increasing attention with respect to its role in the life of plants, but much remains to be learned of its effects on pollination and dispersal biology (see Wyatt, 1982). Little is known of the biology of fagaceous inflorescences or of their relationships with the growth or the reproductive patterns of the trees. Most studies (Abbe, 1974; Macdonald, 1979; Fey & Endress, 1983) have concentrated on the nature of the flower clusters (often called dichasia or partial inflorescences) and cupules. Hjelmqvist (1948) and Soepadmo (1972) briefly reviewed the variety of inflorescences in the Fagaceae. Čelakovský (1889) compared fagaceous inflorescences with betulaceous and juglandaceous ones and enumerated the criteria by which he judged levels of specialization. Jäger (1980) analyzed inflorescences of the Betulaceae, the family perhaps closest to the Fagaceae. For this study, we have analyzed a sample of Fagaceae much larger than those of previous workers, and we here assess their inflorescences in terms of structural as well as functional criteria. Although our emphasis is on Paleotropical species, some species of the northern Temperate Zone are also included. The APPENDIX lists the species studied, as well as the provenance of the specimens.

The family Fagaceae comprises perhaps 900 species. It is most richly represented in eastern and southeastern Asia and the nearby islands of the western Pacific Ocean. In many places the family dominates the forests, and on a worldwide basis it is perhaps second in biomass only to the conifers (Soepadmo, 1972; Heywood, 1978).

In tropical areas the Fagaceae are found from sea level to the frost line, but they are most abundant and often dominant at middle altitudes, where they favor rain forests of little seasonality. There the trees are evergreen and bear mostly entire to slightly sinuate or dentate leaves that sometimes have drip-tips. At higher latitudes in the Northern Hemisphere, the Fagaceae occur in both ever-wet and seasonally dry climates, where they are evergreen or deciduous and their leaves are entire to sharply dentate or deeply lobed. The Southern-Hemisphere genus *Nothofagus* grows in cool montane forests and is mostly evergreen.

Castanea has about ten species in mesic forests of the eastern and southeastern United States, eastern Asia, southern Europe, northern Africa, and the Middle East. All are deciduous. The closely related *Castanopsis* has perhaps 120 species

in eastern and southeastern Asia and western-Pacific islands; there is a single species, *C. chrysophylla*, in montane forests of North America from Washington to California.

Lithocarpus (ca. 300 species) occurs from India to Japan, New Guinea, and Java. It, too, has a single North American representative, *L. densiflora*, in California and southwestern Oregon.

Quercus (ca. 450 species) is widespread and often abundant across all the northern continents, as well as North Africa, at low and middle latitudes. It extends south in the Andean cordillera to about the equator. In Central America, from the Isthmus of Tehuantepec to Colombia, there are 46 species (C. H. Muller, 1942), but in southeastern Asia, from Thailand to Java and Borneo, there are only 19 (Soepadmo, 1972).

Trigonobalanus has three species: *T. verticillata* Forman in southeastern Asia, southern China (Yunnan), and a few islands of the East Indies; *T. dai-changensis* (A. Camus) Forman in Thailand; and *T. excelsa* Lozano, Hernández, & Henao in Colombia.

Forman (1964) and Soepadmo (1972) recognized three subfamilies: Castaneoideae (*Castanea*, *Castanopsis*, *Lithocarpus* s.l.), Quercoideae (*Quercus* s.l., *Trigonobalanus*), and Fagoideae (*Fagus*, *Nothofagus*). Crepet and Daghljan (1980) supported the close affinity of *Quercus* and *Trigonobalanus*, but Lozano and colleagues (1979) placed *Trigonobalanus* alone in Trigonobalanoideae. Kuprianova (1963) suggested that *Nothofagus* constitutes its own family, Nothofagaceae; Nixon (1982) concurred and also suggested betulacean affinities for it.

Asiatic and western-Pacific Fagaceae have been variously interpreted at the species level by Camus (1929, 1934–1954), Barnett (1942, 1944), and Soepadmo (1968, 1970, 1972). The most recent monograph (Soepadmo, 1972) is based on extensive field and herbarium work.

Generic circumscription is complicated in *Castanea*, *Castanopsis*, *Lithocarpus*, and *Quercus* by intermediate characters variously shared among them. *Trigonobalanus* is distinctive. Soepadmo (1972) has acknowledged the essential unity of *Castanea* and *Castanopsis*, the former differing from the latter only in having pistillate flowers always at the base of the spikes and bearing six or more stigmas. He rejected Hjelmqvist's (1948) proposal of generic status (*Chrysolepis*) for the single species of western North American *Castanopsis*, but Forman (1966), Abbe (1974), and others have accepted it. Forman (1964), Soepadmo (1972), and Abbe (1974) recognized *Quercus* as distinct from *Lithocarpus*, despite historical confusion. They noted the constancy of differences including unisexual inflorescences, with the staminate ones pendent (*Quercus*), vs. bisexual erect inflorescences (*Lithocarpus*). There are floral differences as well.

The distinctions between *Lithocarpus* and *Castanopsis* are usually obvious; except for a few species, the genera can be distinguished by the structure of their cupules (Forman, 1966; Soepadmo, 1972).

The affinities of *Fagus* to the other genera—and even to *Nothofagus*—are less certain. In recent decades there has been no confusion concerning the identity of *Fagus* such as there has been about *Castanea*, *Castanopsis*, *Litho-*

carpus, and *Quercus*. These latter four genera form a coherent unit and, with *Trigonobalanus*, are the topic of this paper.

Pollination in Fagaceae is by insects or wind. *Castanea*, *Castanopsis*, *Lithocarpus*, and *Trigonobalanus verticillata* are entomophilous, have scented flowers, and bear erect staminate inflorescences. *Castanea* and *Castanopsis* attract clouds of dipterans and other insects with their heavy, almost unpleasant odor; *Lithocarpus* is more delicately scented. *Trigonobalanus daichangensis* has pendulous staminate catkins and is anemophilous (Hjelmqvist, 1948; Soepadmo, 1972), as are *Quercus*, *Fagus*, and *Nothofagus*. Reports of entomophily in *Quercus* (e.g., Faegri & Van der Pijl, 1979) are perhaps based on species of *Lithocarpus* placed in synonymy with *Quercus*. *Trigonobalanus excelsa*, recently discovered in Colombia (Lozano *et al.*, 1979), is possibly entomophilous because it too has more or less erect staminate inflorescences. Except for the studies of entomophily in *Castanea* by Porsch (1950), Clapper (1954), and Jaynes (1974), there seem to be no definitive assessments of entomophily in the Fagaceae, however. The possibility that some entomophilous species are partially anemophilous (see Proctor & Yeo, 1972; Faegri & Van der Pijl, 1979) should be explored.

Anemophily was present in the family by the Middle Eocene (Crepet, 1979) and was probably a factor leading to its prominence—especially that of *Quercus*—in north-temperate forests (Endress, 1977). Fossils from the Middle Eocene show floral structures almost identical to those of modern Castaneoideae (Crepet & Daghljan, 1980). Thus, the family was well advanced by the Middle Eocene and, in fact, is known from the Campanian and Santonian stages of the Cretaceous (J. Muller, 1981).

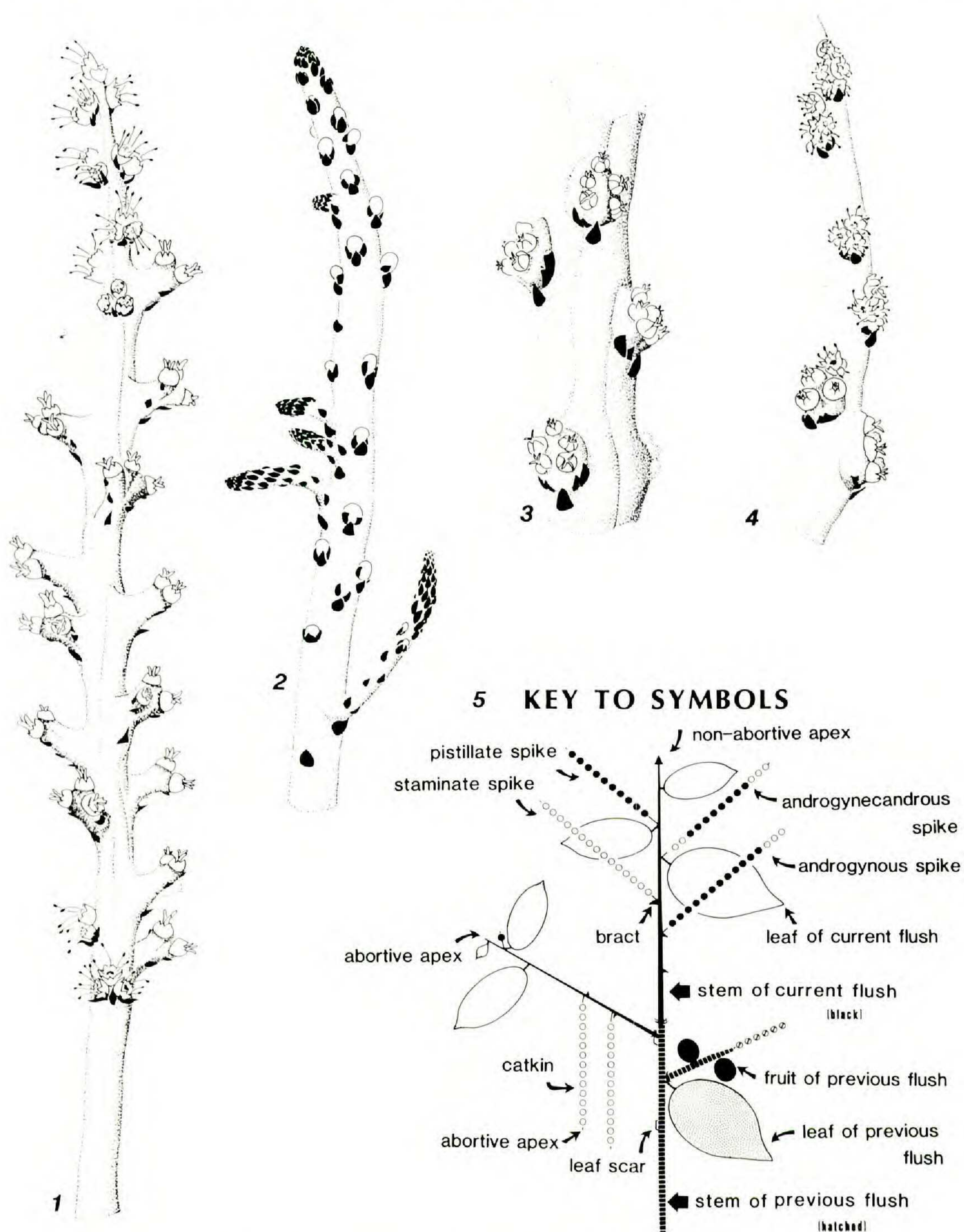
The Fagaceae originated from unknown ancestors that were probably shared with Betulaceae and perhaps other families, but details are unclear. However, the Fagaceae form a large enough group—and one with enough diversity of inflorescence structure—to provide useful internal comparisons that suggest probable evolutionary pathways.

MATERIALS AND METHODS

We examined 126 species in *Castanea*, *Castanopsis*, *Lithocarpus*, *Quercus*, and *Trigonobalanus*, including thousands of specimens from our collections of Asiatic and western-Pacific Fagaceae as well as a few critical North American and European species. We and our colleagues collected in Paleotropical and eastern Asian forests, and for some species we have multiple collections from certain individual trees over a year's time. Most of our Paleotropical specimens have been annotated by Soepadmo, and the nomenclature herein follows his treatment (Soepadmo, 1972).

Each illustration represents an actual specimen at or near anthesis. Because the Fagaceae are so variable, no single figure can depict all the variance in a species or even on an individual tree. For illustration we have chosen species and individuals that best show the diversity of structure.

Where possible, each figure shows current and previous flushes of growth. When leaves from the previous flush were present, as they often were (most



FIGURES 1-5. 1-4, *Lithocarpus*. 1, *L. aggregata*, androgynocandrous spike with pedunculate pistillate and sessile staminate cymules. 2-4, *L. dasystachya*: 2, sylleptic branching of staminate spike with branches arising at sites of cymules; 3, portion of pistillate spike with cymules and some subtending bracts (black); 4, portion of androgynous spike with 1 mixed-sex cymule between staminate and pistillate cymules. 5, key to symbols used in illustrations (open circles, staminate cymules; blackened circles, pistillate cymules).

tropical and many temperate species are evergreen), they are shown shaded (see FIGURE 5). New leaves of the current flush are unshaded, and their relative sizes are approximated. However, because the new leaves continue to expand

after anthesis, many of them would ultimately be relatively larger than shown. No attempt is made to indicate actual leaf shapes or sizes.

Because of the very large number of small flowers in each inflorescence, it is not possible to show individual flowers in these diagrams. Therefore, staminate and pistillate cymules are indicated with open and blackened circles, respectively. The relative lengths of the rows of circles suggest only the relative lengths of the floriferous axes, not the actual numbers of flowers. In most cases the number of staminate cymules and flowers is much larger (sometimes by factors of hundreds) than the number of open circles.

DEFINITIONS

There are no standard, universal definitions for inflorescences like those existing for flowers, and it is unlikely that such definitions are possible. Rather, each group requires careful review of both the applicable inflorescence terminology and the accompanying definitions. Even the term "inflorescence" cannot be applied equivalently in all angiosperm taxa. Definitions applied at the level of flowering plants may be descriptively useful but often produce little evolutionary information.

In the Fagaceae, as in other angiosperms and especially in trees and shrubs, delimitation of inflorescences is not always obvious and no terminology exists that adequately covers all configurations. We use *total inflorescence* for all the synchronously produced floriferous axes on a *shoot system*, whether or not they are aggregated into a defined "synflorescence" (Troll, 1964) or "conflorescence" (Briggs & Johnson, 1979). A *shoot system* is here intended to mean a major indeterminate axis that clearly has a *leader* and reproductive branches bearing *spikes* or *catkins* (erect or pendent floriferous axes, respectively). The total inflorescence can include branches produced by nonresting buds of the current flush (*syllleptic* branches), those produced by axillary buds of the previous flush (*proleptic* branches), or both.

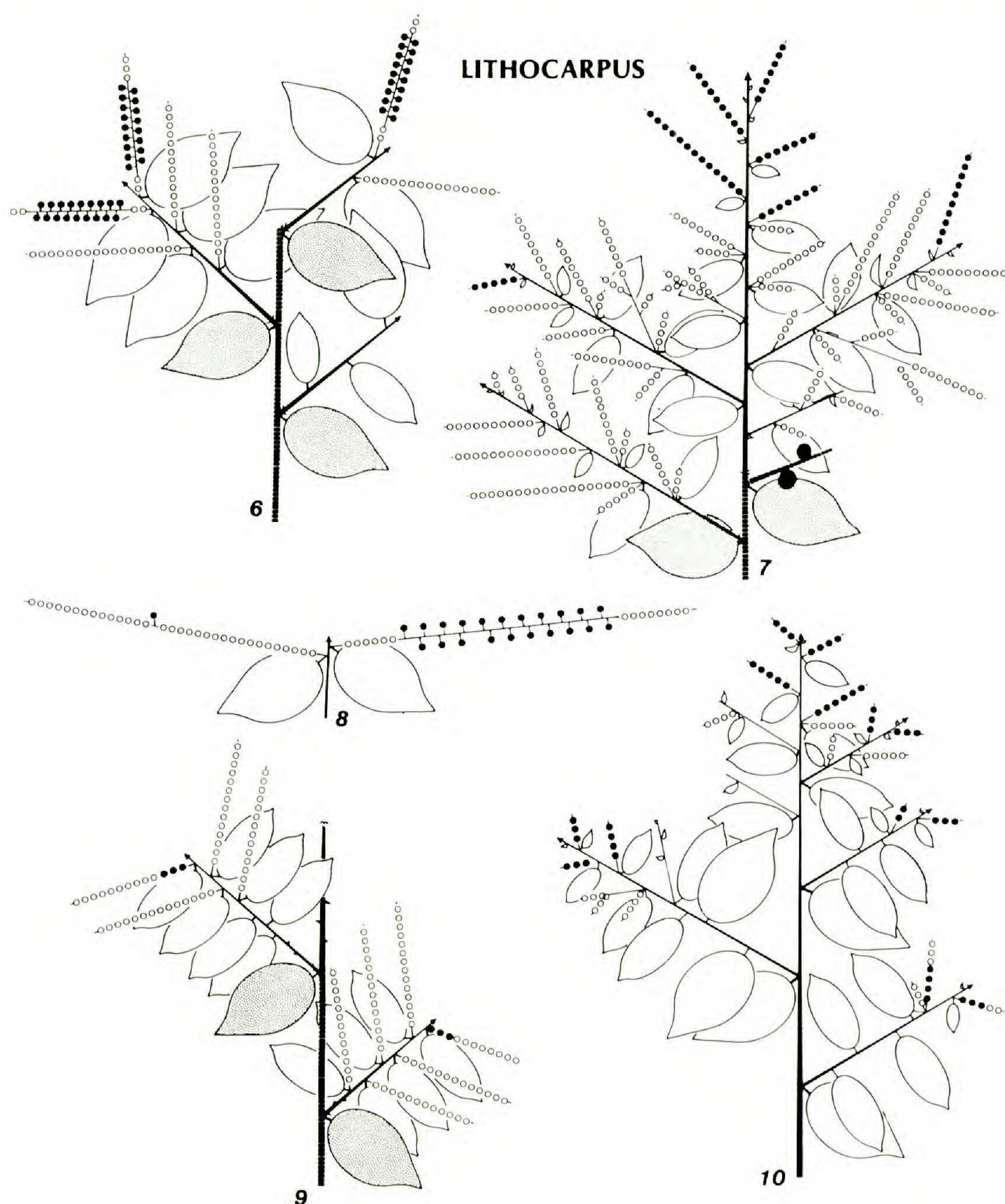
No axis (including spikes and catkins) that we examined in this study terminated in an abortive or functional floral bud. In the parlance of Briggs and Johnson (1979), all of these axes are blastotelic (terminate in a nonfloral bud); some are auxotelic (producing continuing growth with or without a dormant period; *indeterminate*), while others are anauxotelic (not continuing growth; *determinate*). Spikes and catkins are determinate, as are some vegetative branches; the leader and some vegetative branches are indeterminate.

Bract refers to any nonfoliar leaf homologue in any branch order. *Foliose* defines an axis bearing only normal foliage leaves, while *folio-bracteose* indicates axes with both bracts and leaves. *Bracteose* axes bear only bracts at the nodes.

OBSERVATIONS

DISTRIBUTION OF FLOWERS ON SPIKES AND CATKINS

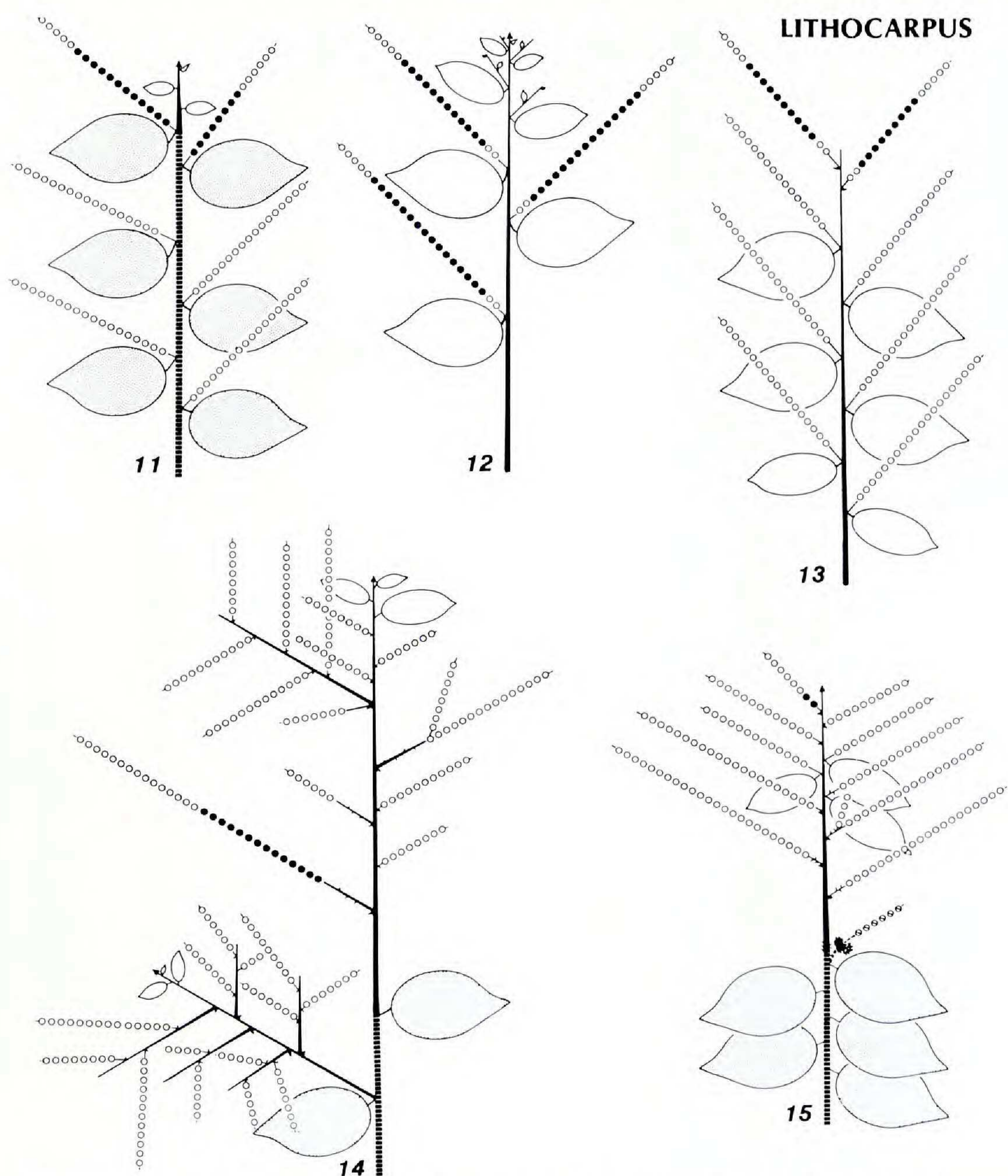
Flowers are always arranged singly or in groups of 2 to 25 or more along the axis of a spike or catkin. Although the groups of florets are often called "di-



FIGURES 6–10. *Lithocarpus*: 6, *L. aggregata*, with distinctly pedunculate pistillate cymules; 7, *L. nodosa*, with sylleptic and proleptic branching; 8, *L. sootepensis*, with pedunculate pistillate cymules; 9, *L. amygdalifolia*; 10, *L. havilandii*, showing sylleptic branching.

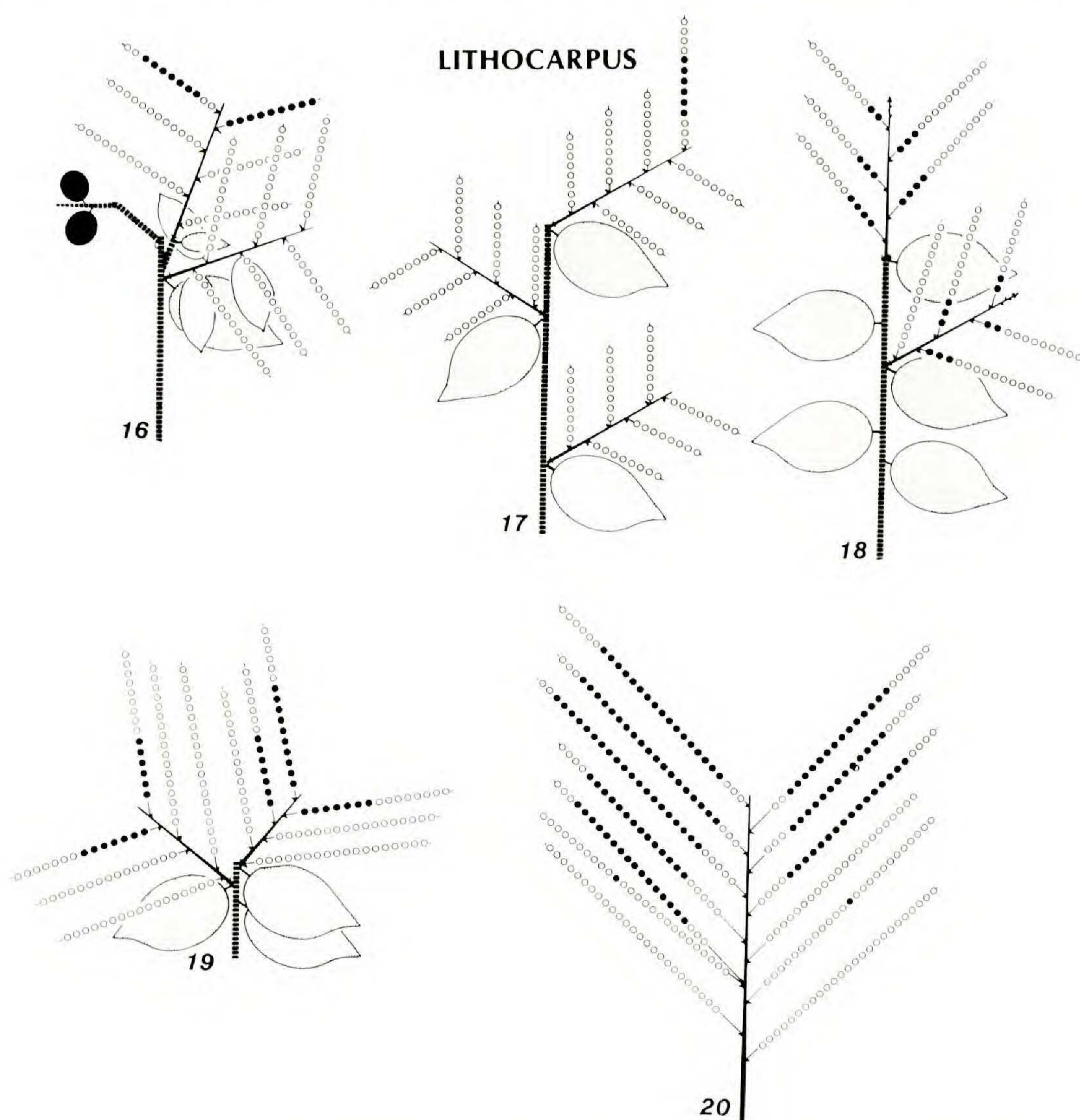
chasia" in the literature, they are sometimes monochasial. Less specific terms are "cymule" and "partial inflorescence." The details are often obscure because of miniaturization and cupule development, and the diverse theories concerning the basic character of the cupule necessitate caution in the assignment of a specific branching pattern to the cymules (see Fey & Endress, 1983). The cymules are short-shoots on the elongate axis of the spike or catkin, which is a long-shoot.

Spikes are entirely staminate, entirely pistillate, androgynous (with the sta-



FIGURES 11–15. *Lithocarpus*: 11, *L. ewyckii*, with proleptic axillary spikes synchronous with beginnings of new shoot growth; 12, *L. bolovensis*, with sylleptic androgynous spikes; 13, *L. thomsonii*; 14, *L. cooperta*; 15, *L. densiflora*, with 1 branched staminate spike.

minate cymules distal to the pistillate—see, for example, FIGURES 5, 11), gynecandrous (with the pistillate cymules in the distal position—e.g., FIGURE 27), or androgynecandrous (with the pistillate cymules between groups of staminate ones—e.g., FIGURES 5, 6). Occasionally staminate and pistillate cymules are mixed or parallel along short segments of the spikes. Perfect flowers and mixed-sex cymules (FIGURE 4) are common and often occur at the boundary between staminate and pistillate segments of a spike. Catkins, which occur only in *Quercus* (FIGURES 39, 44–66) and *Trigonobalanus daichangensis* (FIGURE 69), are always staminate.



FIGURES 16–20. *Lithocarpus*: 16, *L. turbinata*; 17, *L. bennettii*; 18, *L. kodaihoensis*; 19, *L. echinocarpa*; 20, *L. curtisii*.

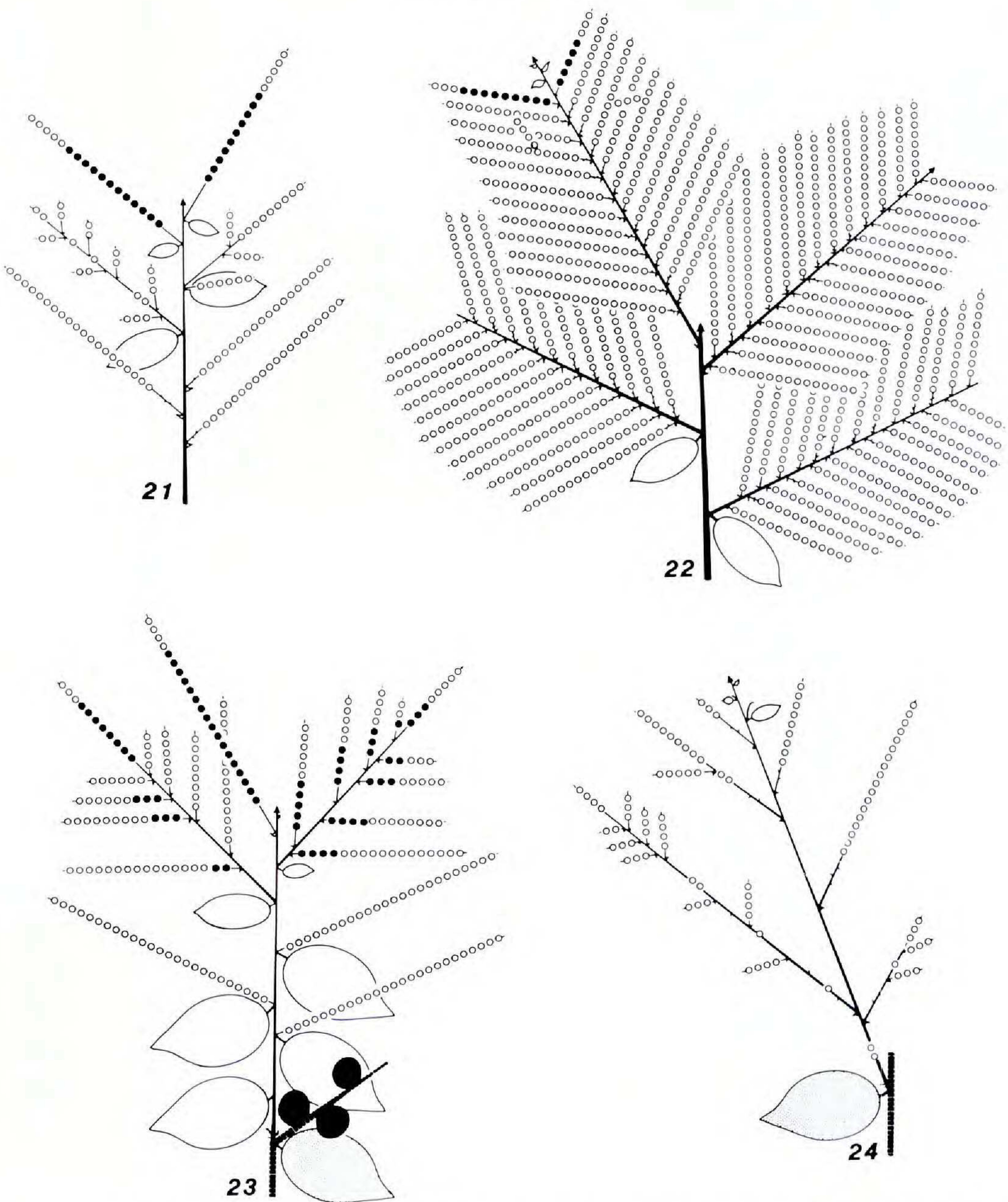
Each cymule is subtended by one or more bracts (FIGURES 1–4), but these are not illustrated in FIGURES 5–70.

GROWTH PATTERNS AND THE DISTRIBUTION OF SPIKES AND CATKINS

Tropical Fagaceae often have several flushes a year, most of them floriferous but not always synchronous on a tree or among conspecifics of an area. Northern Fagaceae are usually presumed to have a single flush, but we observed as many as five in five species of *Quercus* during a wet summer in Nebraska. In these the flushes were separated by one- to three-week intervals, and only the first of the season was floriferous; proleptic branches occurred in all but the final flush.

Shoots, leaves, spikes, and catkins are produced synchronously. Extension growth is monopodial from terminal buds of the previous flush. Dormant lateral buds of the previous flush also can produce proleptic extension growth, inflo-

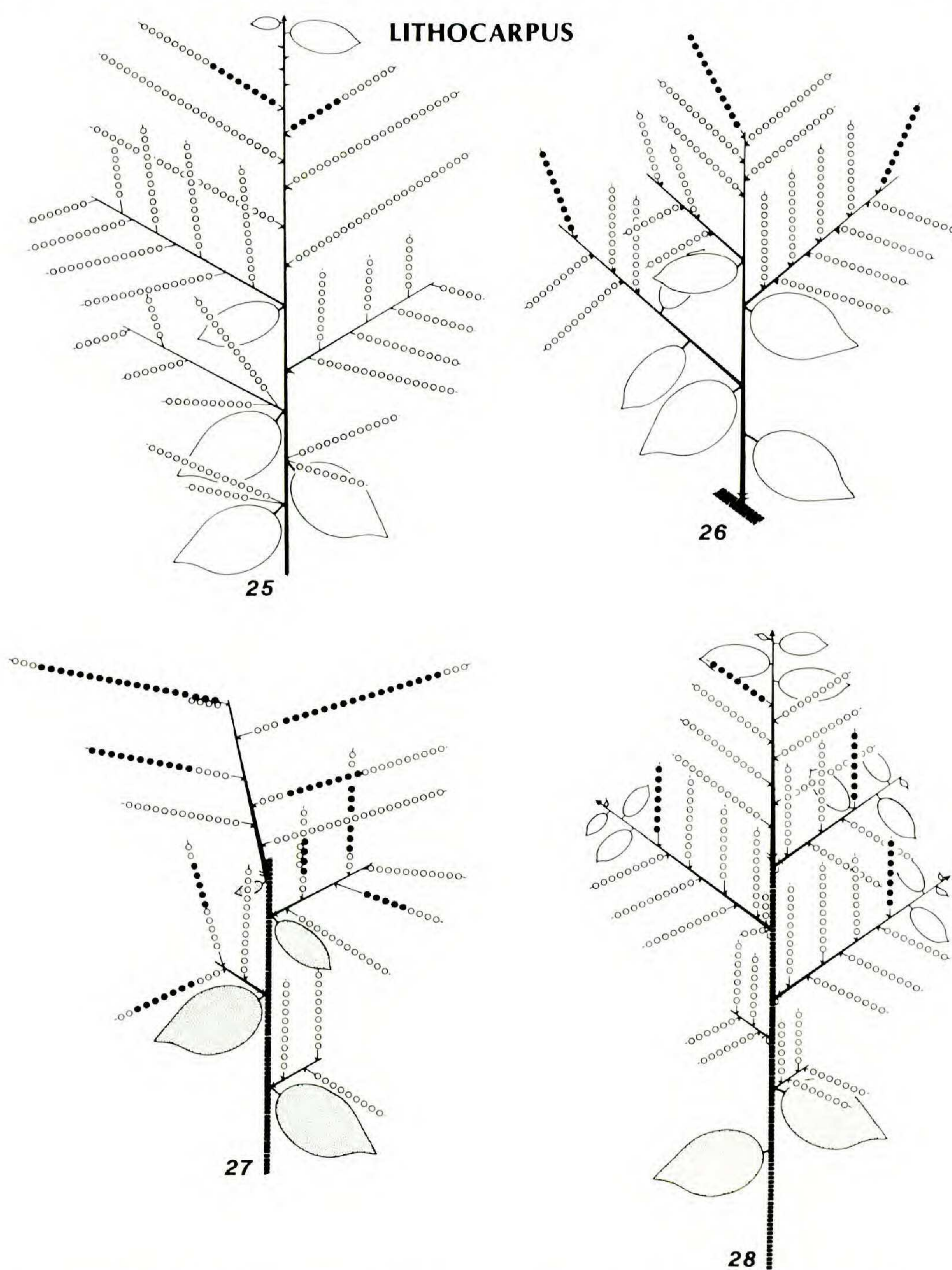
LITHOCARPUS



FIGURES 21–24. *Lithocarpus*. 21, 22, *L. sundaica*: specimen with 2 branched staminate spikes; 22, specimen with 4 large reproductive branches, the distal 2 indeterminate, the uppermost 1 with few weakly branched staminate spikes and some pistillate dichasia. 23, *L. lampadaria*, with 2 branched bisexual spikes. 24, *L. cooperta*, with 3 branched staminate spikes.

rescences, or both. The growth of many, if not all, species of *Castanea*, *Castanopsis*, *Lithocarpus*, and *Quercus* conforms to Rauh's model (see Hallé *et al.*, 1978), in which the rhythmic monopodial growth pattern of the trunk is repeated in the branches. *Trigonobalanus verticillata* conforms to Attim's model (Hallé *et al.*, 1978), which resembles Rauh's model except that growth is continuous (nonrhythmic).

Nearly every leaf has a spike or reproductive branch in its axil at some time,

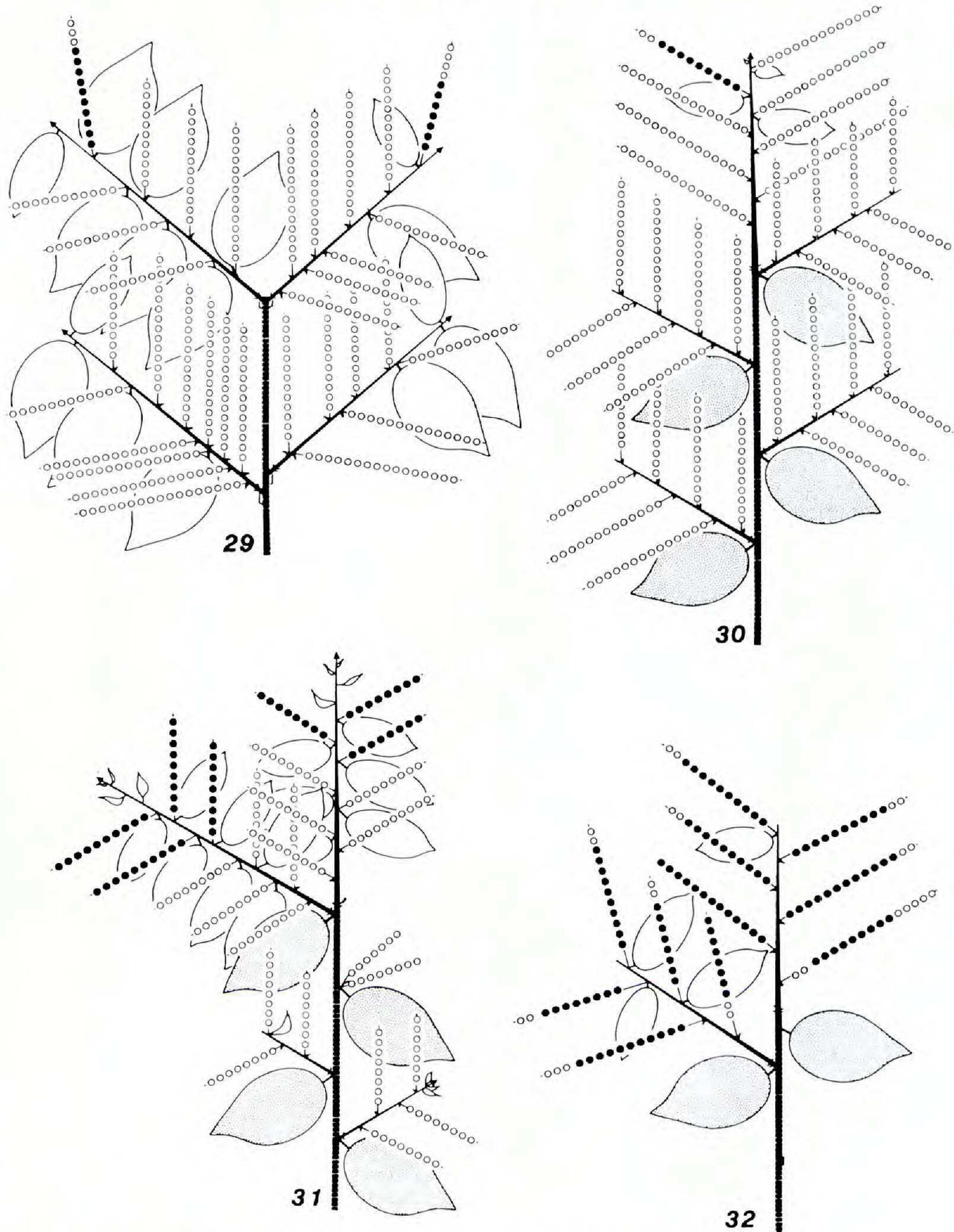


FIGURES 25–28. *Lithocarpus*: 25, *L. nieuwenhuisii*; 26, *L. caudatifolia*; 27, *L. curtisii*; 28, *L. kawakamii*.

and in that sense most of the tree is once part of an inflorescence. In some species the foliage leaves subtend individual spikes (e.g., FIGURES 11–13, 36, 40–45). The leader and most foliose branches are indeterminate. Indeterminate folio-bracteose branches are distally foliose and proximally bracteose (e.g., FIGURES 29, 35, 39).

Bracteose reproductive branches are often determinate (e.g., FIGURES 14, 16–18). Those bearing staminate spikes and catkins are shed soon after anthesis,

CASTANOPSIS

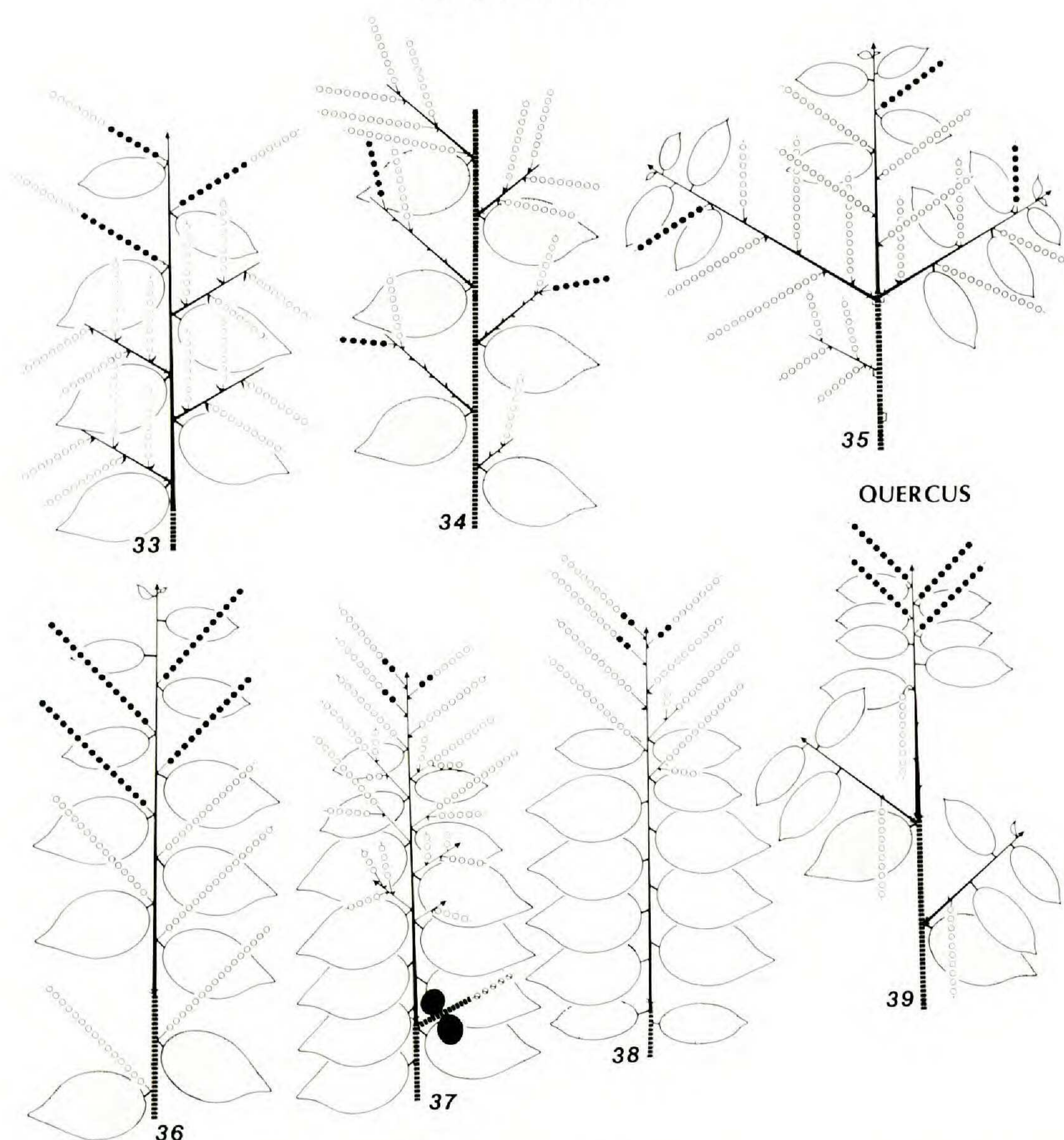


FIGURES 29–32. *Castanopsis*: 29, *C. inermis*; 30, *C. fissa*; 31, *C. acuminatissima*; 32, *C. rhamnifolia*.

while those with pollinated pistillate flowers are retained but usually drop their staminate spikes or flowers. These determinate branches are sometimes present on the same axis with indeterminate ones (e.g., FIGURES 22, 28, 31), in which case they are usually proximal and the indeterminate branches distal on the axis. Furthermore, they are often smaller than the distal branches and bear fewer spikes with fewer flowers.

Sometimes sylleptic spikes and reproductive branches are accompanied by similar proleptic spikes and branches in a shoot system (e.g., FIGURES 16–19,

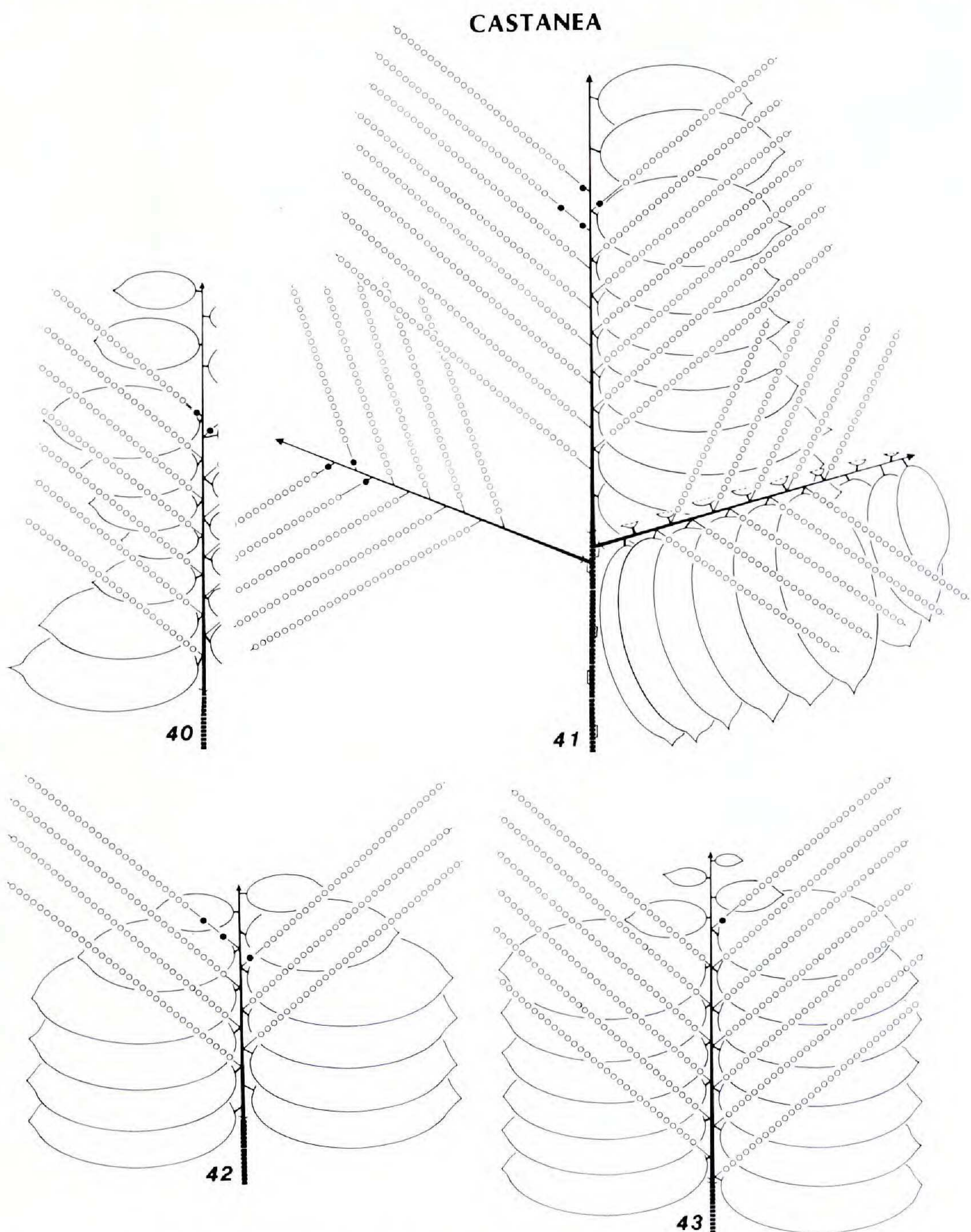
CASTANOPSIS



FIGURES 33–39. *Castanopsis* and *Quercus*: 33, *C. brevispina*; 34, *C. subacuminata*; 35, *C. stipitata*; 36, *C. stellatospina*; 37, 38, *C. chrysophylla*; 39, *Q. uraiana*.

30–32, 56). These proleptic structures are often strictly staminate, but the distal ones sometimes have a few pistillate flowers (e.g., FIGURES 6, 16–19, 31, 41, 46).

In some Fagaceae full repetition of the leader's growth pattern, floral display, and sex distribution is obvious in the branches, whether they are sylleptic or proleptic (FIGURES 10, 28, 31, 32, 41, 70A). In others the lateral branches are repetitive but determinate (FIGURE 26). More often, there is a basipetal gradient of decreasing similarity between the leader and its branches, both sylleptic and proleptic (FIGURES 25, 27–31, 33–35, 70C, D). The most extreme manifestation of this gradient has small, determinate, bracteose branches bearing only staminate spikes or catkins (e.g., FIGURES 25, 33–35, 44, 60, 70E–G). The middle branches, between the leader and the proximal branches, are frequently inter-

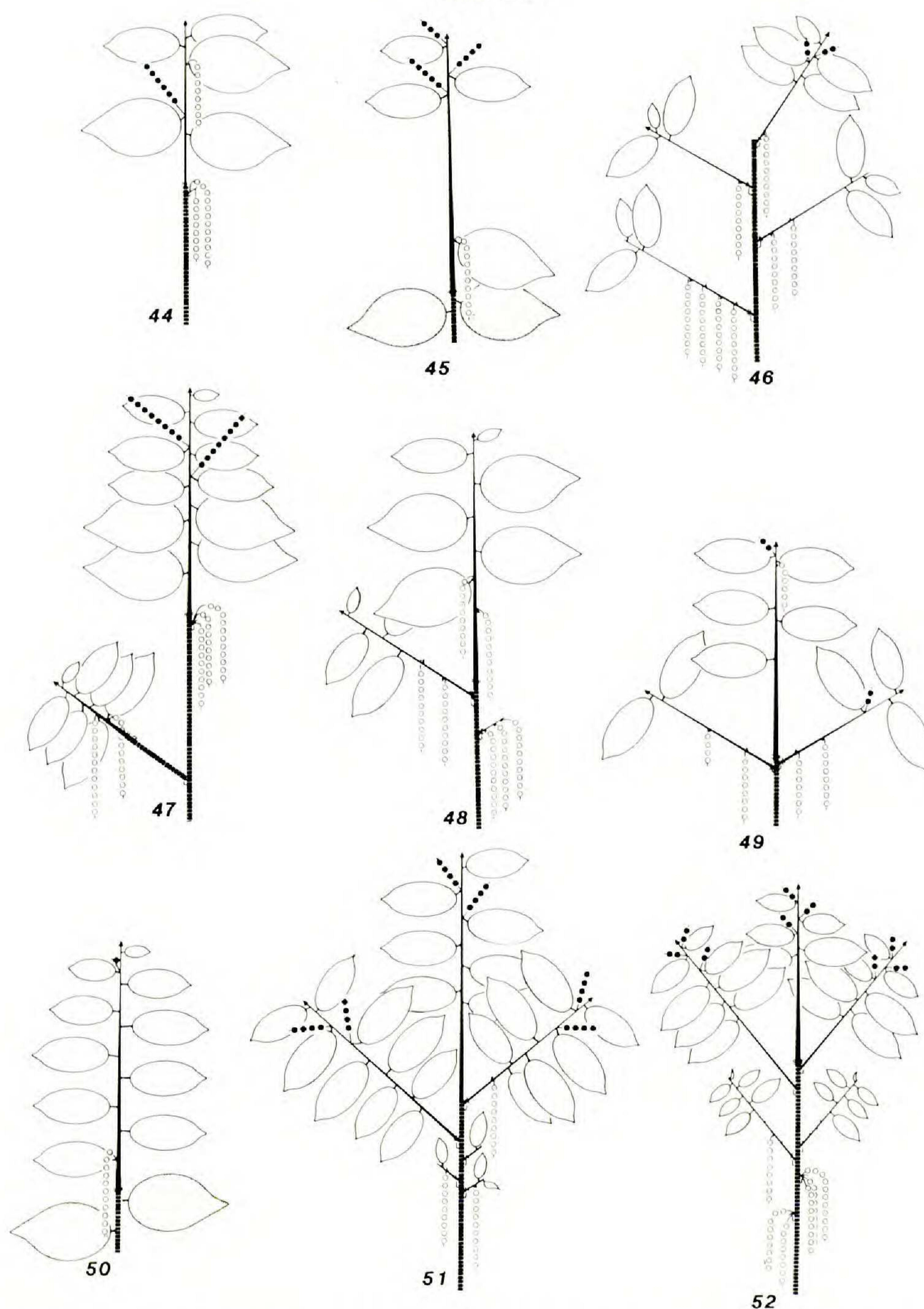


FIGURES 40-43. *Castanea*: 40, 41, *C. mollissima*; 42, *C. crenata*; 43, *C. dentata*.

mediate in structure as well; they are often folio-bracteose, bear a few pistillate flowers, and may be determinate or indeterminate.

The greatest differentiation between the leader and its branches occurs in *Quercus*, where in the most extreme cases some reproductive branches are distinctly short-shoots, are always proleptic and bracteose, bear only staminate catkins, and are entirely deciduous. The leader is foliose and bears pistillate spikes and sometimes also staminate catkins (FIGURES 44, 47, 52, 66, 70F, G). Less extreme differentiation is shown by branches that have catkins axillary to the proximal leaves or bracts while the distal part of the axis is foliose,

QUERCUS

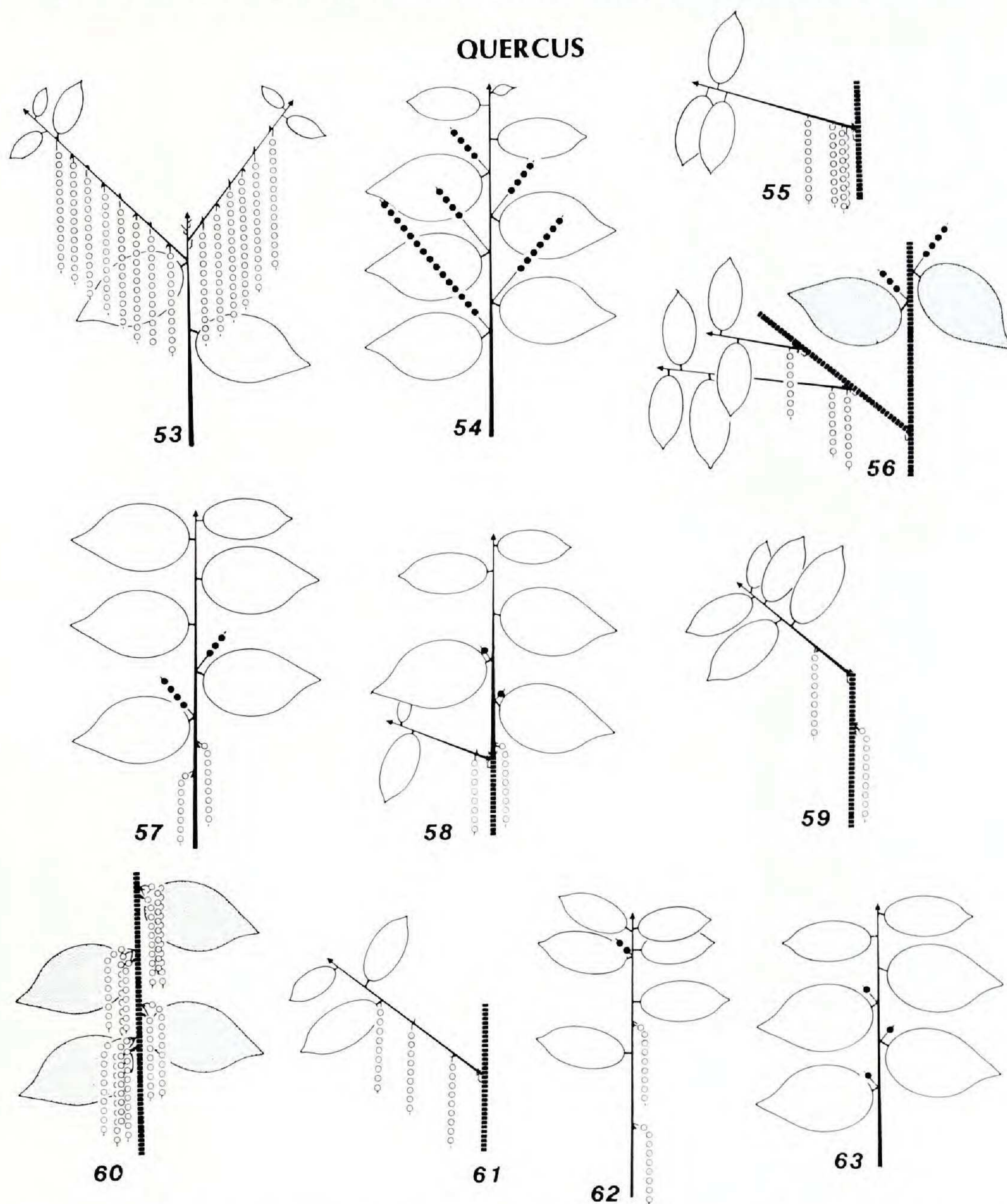


FIGURES 44–52. *Quercus*: 44, 47, *Q. glauca*; 45, *Q. championii*; 46, *Q. stenophylloides*; 48, *Q. morii*; 49, *Q. phillyraeoides*; 50, *Q. acuta*; 51, *Q. myrsinaefolia*; 52, *Q. gilva*.

sterile, and determinate or indeterminate (FIGURES 46–49, 55, 56, 64, 65). Sometimes several degrees of differentiation between leader and branches exist on the same tree.

DISTRIBUTION OF THE SEXES IN THE SHOOT SYSTEM

Pistillate flowers, if present at all in a shoot system, are borne on distal spikes; the proximal spikes are staminate (FIGURES 6–13, 16–23, 25–52, 54, 56–58,

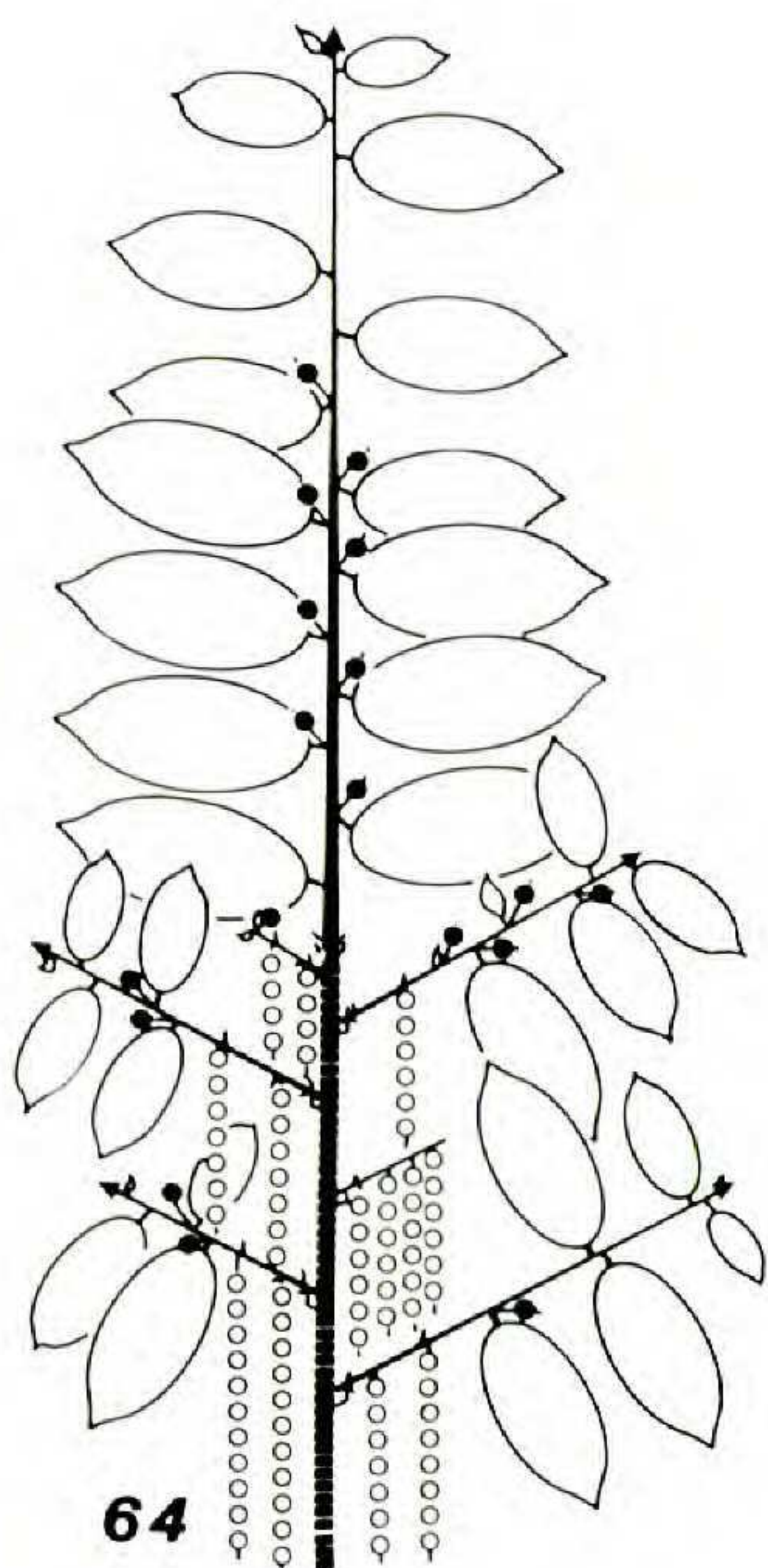


FIGURES 53–63. *Quercus*: 53, *Q. kingiana*; 54, *Q. brandisiana*; 55, *Q. cf. chapensis*; 56, *Q. cambodiensis*; 57, *Q. mespilifolioides*; 58, *Q. griffithii*; 59, *Q. serrata*; 60, *Q. championii*; 61, *Q. kinabaluensis*; 62, *Q. valdinervosa*; 63, *Q. elmeri*.

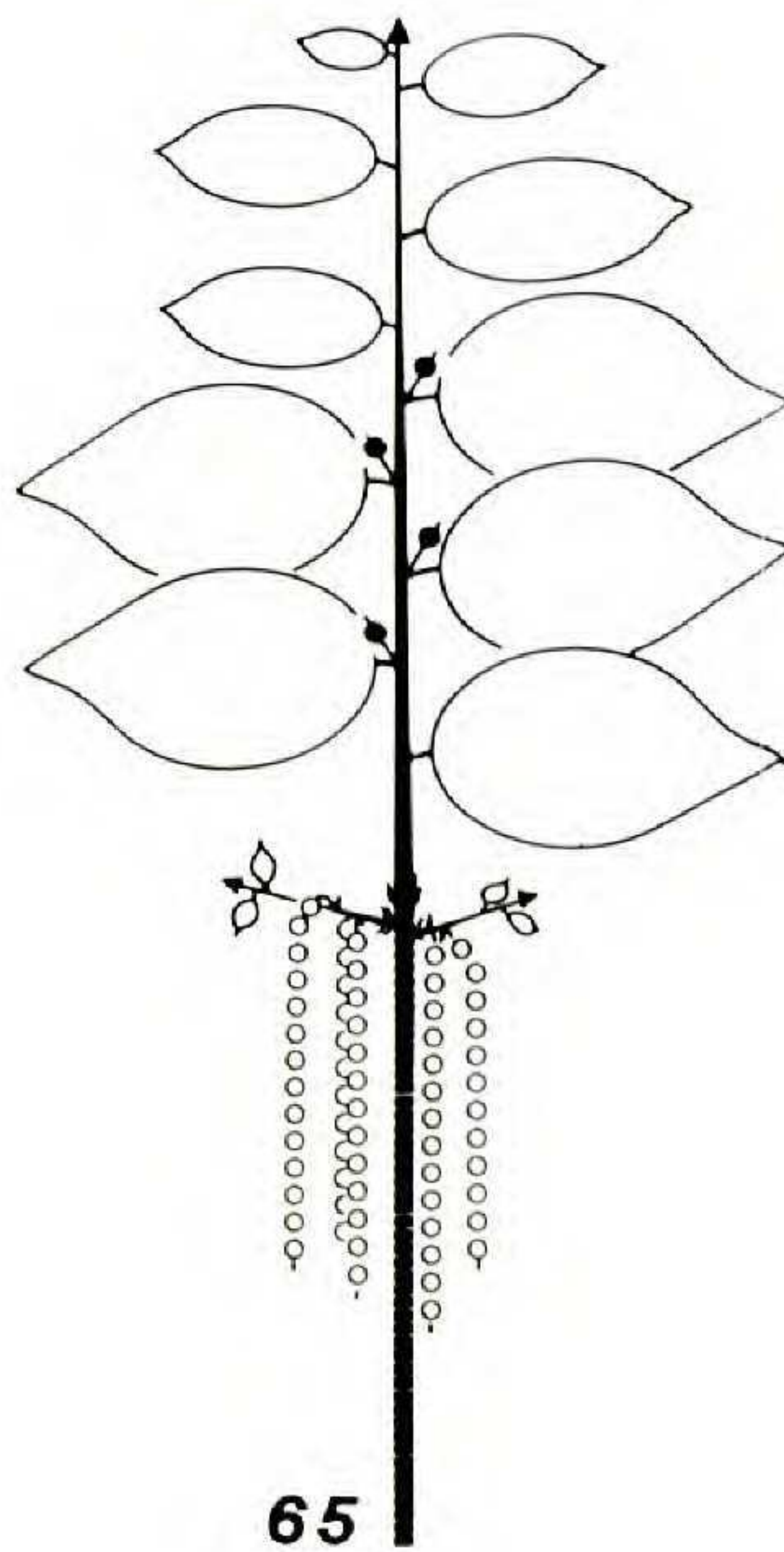
62–66, 69, 70). Sometimes the leader has more pistillate flowers on more spikes than its branches (FIGURES 7, 10, 30, 70A–C), but in other cases the distribution of pistillate flowers is about equal on leader and branches (e.g., FIGURES 18, 26, 28, 31, 32). In any case, a clear acropetal gradient of increasing “femaleness” is evident in almost every species examined. This gradient is variously expressed in the leader, in the branches, and/or in the total inflorescence, and it complements the basipetal gradients of reduction of leaves to bracts and loss of indeterminacy in branches.

In *Quercus* and *Trigonobalanus daichangensis* the sexes are almost always borne on separate axes (FIGURES 44–66, 69). Pistillate spikes (which sometimes

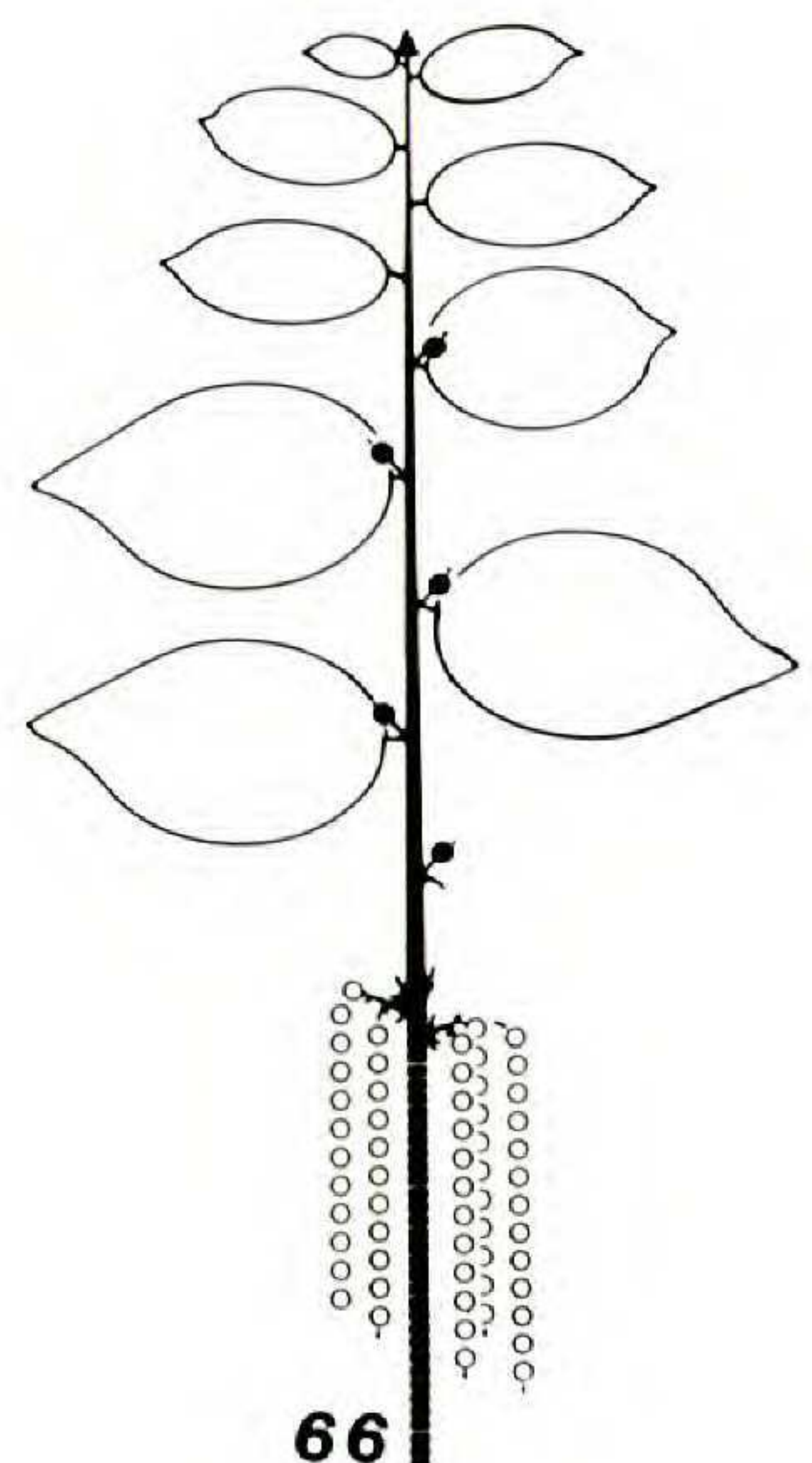
QUERCUS



64

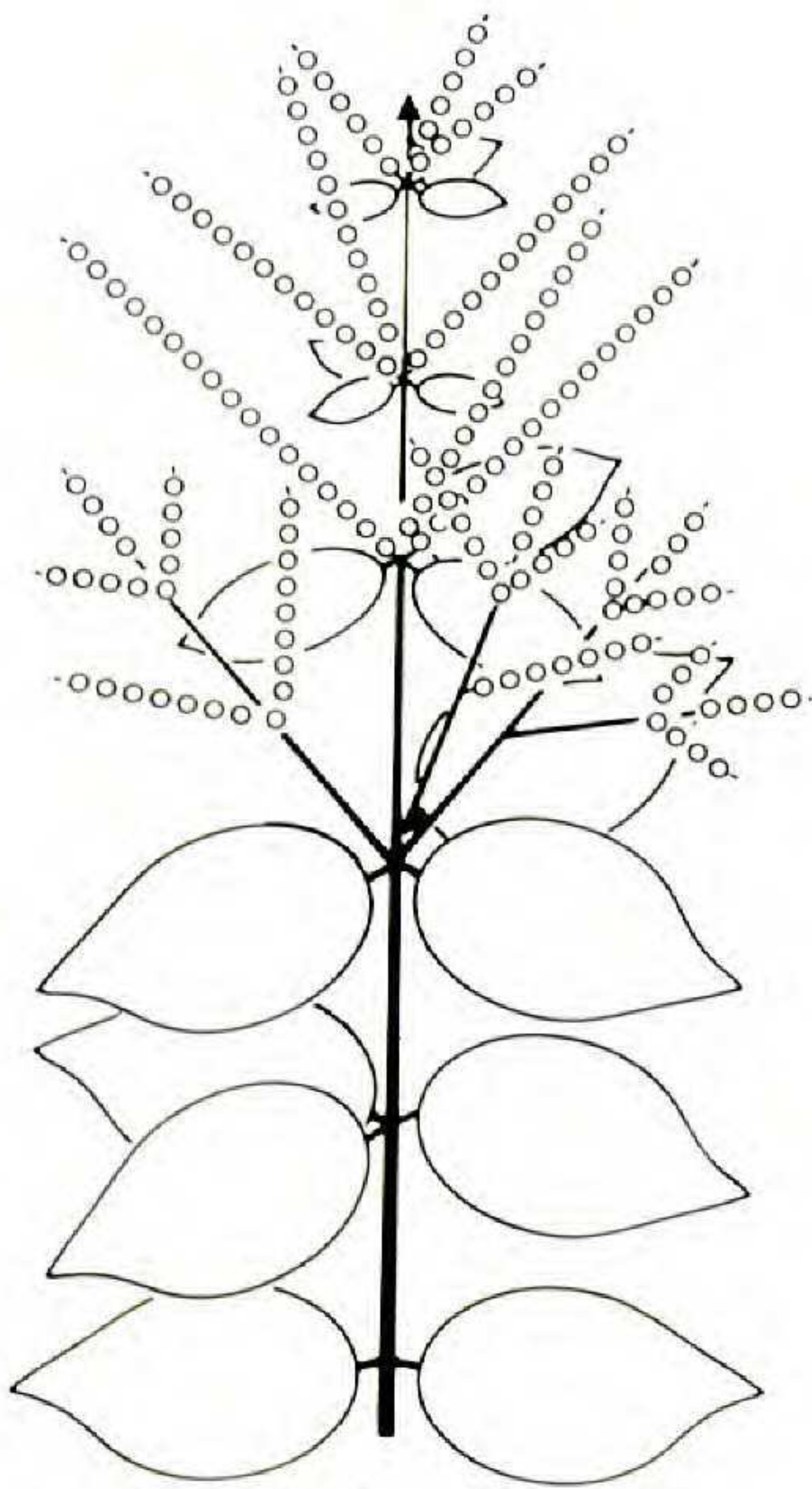


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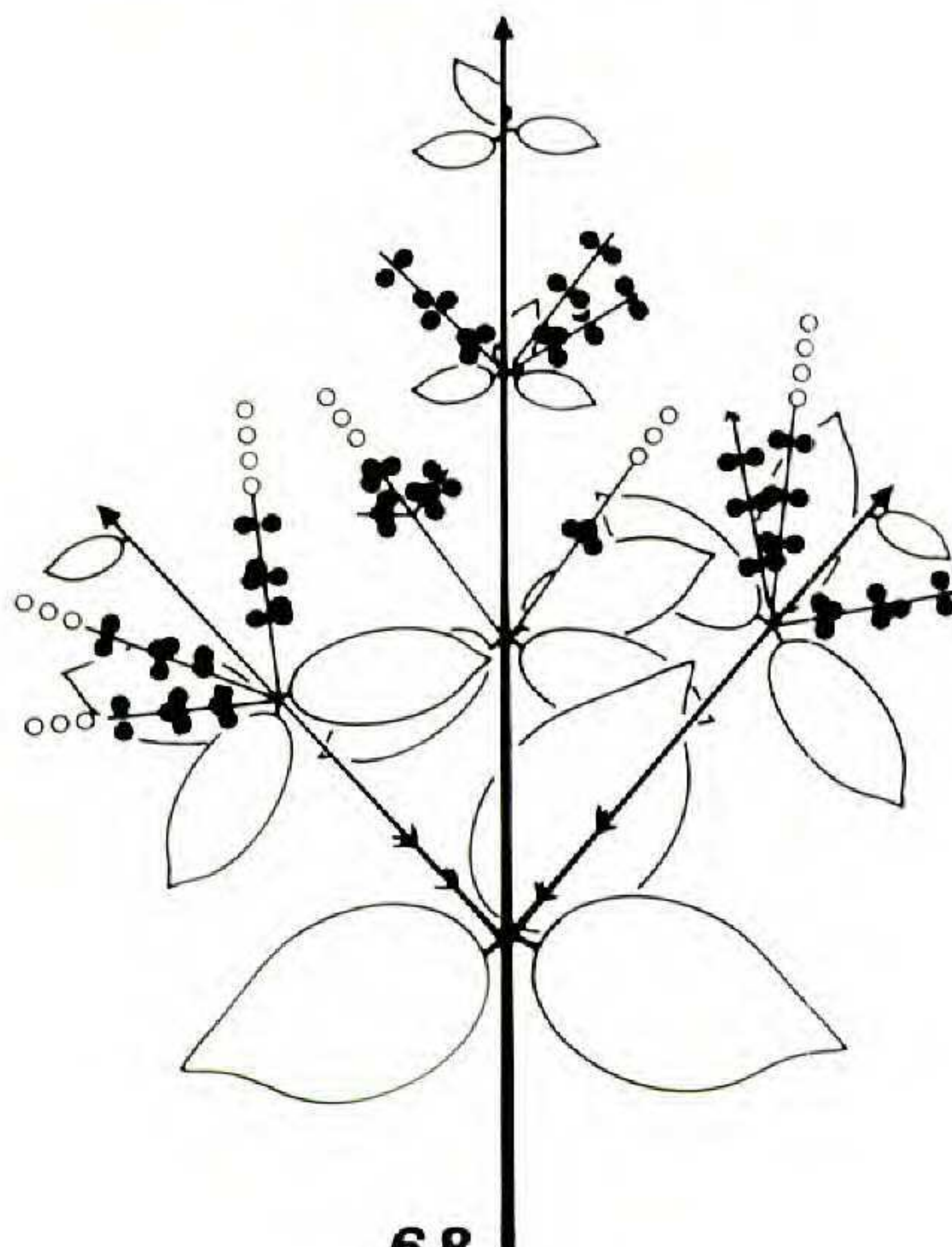


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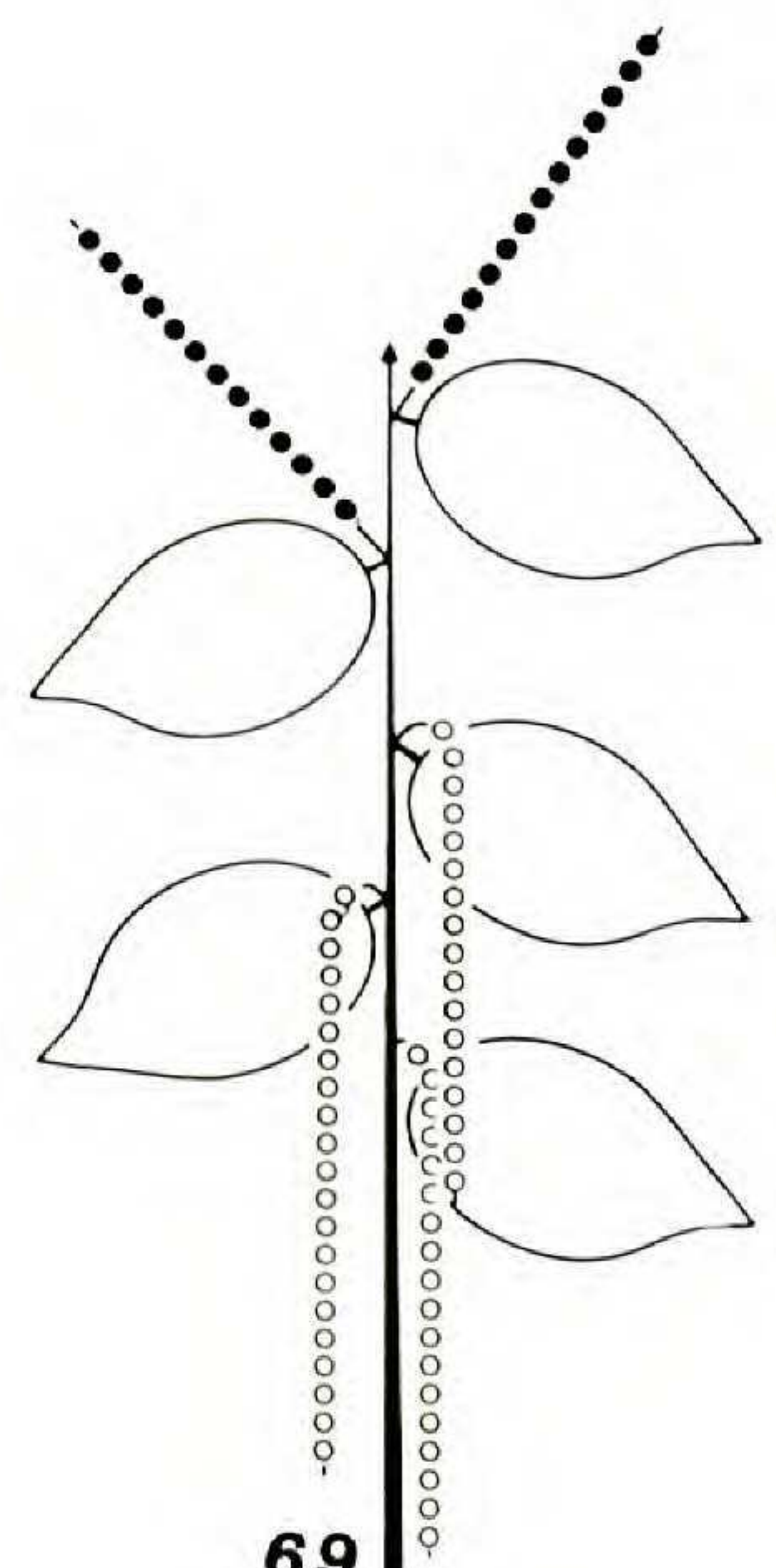
TRIGONOBALANUS



67



68



69

FIGURES 64–69. *Quercus* and *Trigonobalanus*: 64, *Q. imbricaria*; 65, 66, *Q. borealis*; 67, 68, *T. verticillata*; 69, *T. daichangensis* (after Forman, 1964).

exist as a single cymule or flower) are invariably distal and are nearly always subtended by a leaf. Staminate catkins occur singly in the axil of a leaf or bract, mostly in the proximal part of the shoot system (FIGURES 44–53, 55–59, 61, 64–66, 69). They are shed soon after anthesis. Catkin-bearing short-shoots are proleptic (e.g., FIGURES 44, 47, 48, 52) and are also shed soon after anthesis.

In *Trigonobalanus verticillata* some shoots bear only staminate spikes, while others have androgynous ones (FIGURES 67, 68); our specimens and observations are inconclusive as to the existence of a sex gradient in the total inflo-

rescence. Likewise, information about sex distribution in *T. excelsa* is ambiguous. According to Lozano and colleagues (1979), staminate and pistillate inflorescences are borne separately on the tree.

In the northern genus *Castanea* (FIGURES 40–43) the ratio of staminate to pistillate cymules is higher than in *Castanopsis* or *Lithocarpus*. However, the only two American species of the latter two genera, *Castanopsis chrysophylla* (FIGURES 37, 38) and *Lithocarpus densiflora* (FIGURE 15) also have such a higher ratio, and they too are northern. This ratio apparently also exists in *Quercus*, where the northern species bear fewer pistillate cymules on a branch than do many tropical species.

SYLLEPSIS OF THE SPIKES

The spikes contain two kinds of axes: 1) an elongate primary axis or long-shoot to which the 2) cymose short-shoots are racemosely attached. Second-order sylleptic long-shoots are rather common in the staminate spikes of *Lithocarpus* and *Castanopsis chrysophylla* (FIGURES 7, 21–24, 37, 38, 67) and are occasional in *Castanea*. An occasional bisexual spike also has sylleptic branches (FIGURE 23). Such sylleptic branching produces ramified spikes with branches at what would otherwise be sites of cymules and each second-order long-shoot is subtended by a primary bract in the proper phyllotactic position (FIGURE 2). The truly sylleptic nature of this branching is evidenced in FIGURE 2, where second-order branches are appearing on an immature primary axis.

Sylleptically branched spikes differ from bracteose reproductive branches (as defined above) in that they bear dichasia on the primary axis and terminate in a floriferous axis. There is no functional or abortive bract-clad apex of the kind found on typical vegetative branches.

In some instances, typical bracteose reproductive branches bear a distal spike that overtops the primary axis (see FIGURE 26), and the abortive apex is then apparently lateral. Although such a branch appears to be a sylleptically branched spike, it is readily distinguished from a truly sylleptic spike by the large, lateral, bract-clad abortive apex.

DISCUSSION

Studies of floral development and morphology have produced a large body of literature on evolutionary pathways and adaptations in flowers. Although literature concerning inflorescences is less definitive, many of the same forces behind floral evolution are clearly also involved in inflorescence evolution, with analogous morphological results. Flowers and inflorescences share such major functions as effecting pollination and nurturing and disseminating seeds and fruits.

Such well-known floral evolutionary phenomena as pleiomery, oligomery, heterochrony, changes in size and symmetry, protogyny and protandry, and transfer of function are also found in inflorescences. We can therefore apply some of the principles of floral evolution to inflorescences.

In the history of plants, vegetative and reproductive functions became sep-

arated and strobili, flowers, and inflorescences were produced. Further phylogenetic differentiation in flowers was by continued separation of functions, producing such advanced features as imperfect flowers, dioecy, anemophily, or elaborate forms of entomophily, and a host of attendant morphological features. These have appeared repeatedly and independently in diverse angiosperms responding to similar evolutionary pressures. Apparent reversal of these trends, such as anemophily reverting to entomophily, involves further modifications of existing structures and behaviors in response to new evolutionary pressures similar to ancestral ones.

There is genetic and ecological evidence that the outcrossing produced by many of these structures and pollination systems is advantageous to the species. Temporal and/or spatial separation of the sexes is most evident in highly evolved plants such as the Fagaceae.

In the Fagaceae some evolutionary patterns have recurred at successively higher levels of morphological organization. The separation of sexes into different flowers, which is almost total in extant Fagaceae, preceded separation of imperfect flowers on the spike, of staminate from pistillate spikes on the same shoot, and of shoots bearing only staminate or pistillate spikes. Many stages of these events occur in various combinations in living Fagaceae, but of the genera studied, only *Quercus* and a few species in other genera show them in their fullest expression.

Paralleling these events are the beginnings of protandry at the inflorescence level. This is a natural consequence of the acropetal ontogeny of shoots and spikes, the acropetal anthesis of flowers, and the restriction of female flowers to distal regions of the shoots. None of the genera studied, however, is morphologically dioecious, although some may approach functional dioecism. The frequent lack of synchrony among adjacent conspecific individuals (which we often saw in the field) contributes another dimension to incipient functional dioecism.

The Fagaceae also show stages of separation of reproductive from vegetative functions. Foliose reproductive branches are usually indeterminate and perform all functions, including extension growth. Merely bracteose reproductive branches are mostly determinate and abscise quickly if they bear only staminate spikes, but they are determinate to indeterminate if they have pistillate flowers.

Compared with tropical species of Fagaceae, more northerly members show reduced or, most often, no syllepsis in their shoots or spikes. (The cymulose short-shoots are, of course, sylleptic on their long-shoots, as are spikes on the shoots that bear them.) The spikes of *Castanopsis chrysophylla* and *Lithocarpus densiflora* (and occasionally *Castanea*) show it only weakly. Even within *Castanopsis* and *Lithocarpus*, there is probably a general loss of syllepsis as one moves from the tropics into the Northern Hemisphere, while the strictly extratropical *Castanea* has nearly lost it altogether. In *Quercus* there is none in the catkins of any species we studied, and only one of our species, *Q. kingiana* from Burma (FIGURE 53), showed vegetative syllepsis.

These observations are consistent with the well-known decline of syllepsis in trees and shrubs in general as one moves northward from the tropics. It is thus possible that syllepsis is an ancestral condition in the Fagaceae and other

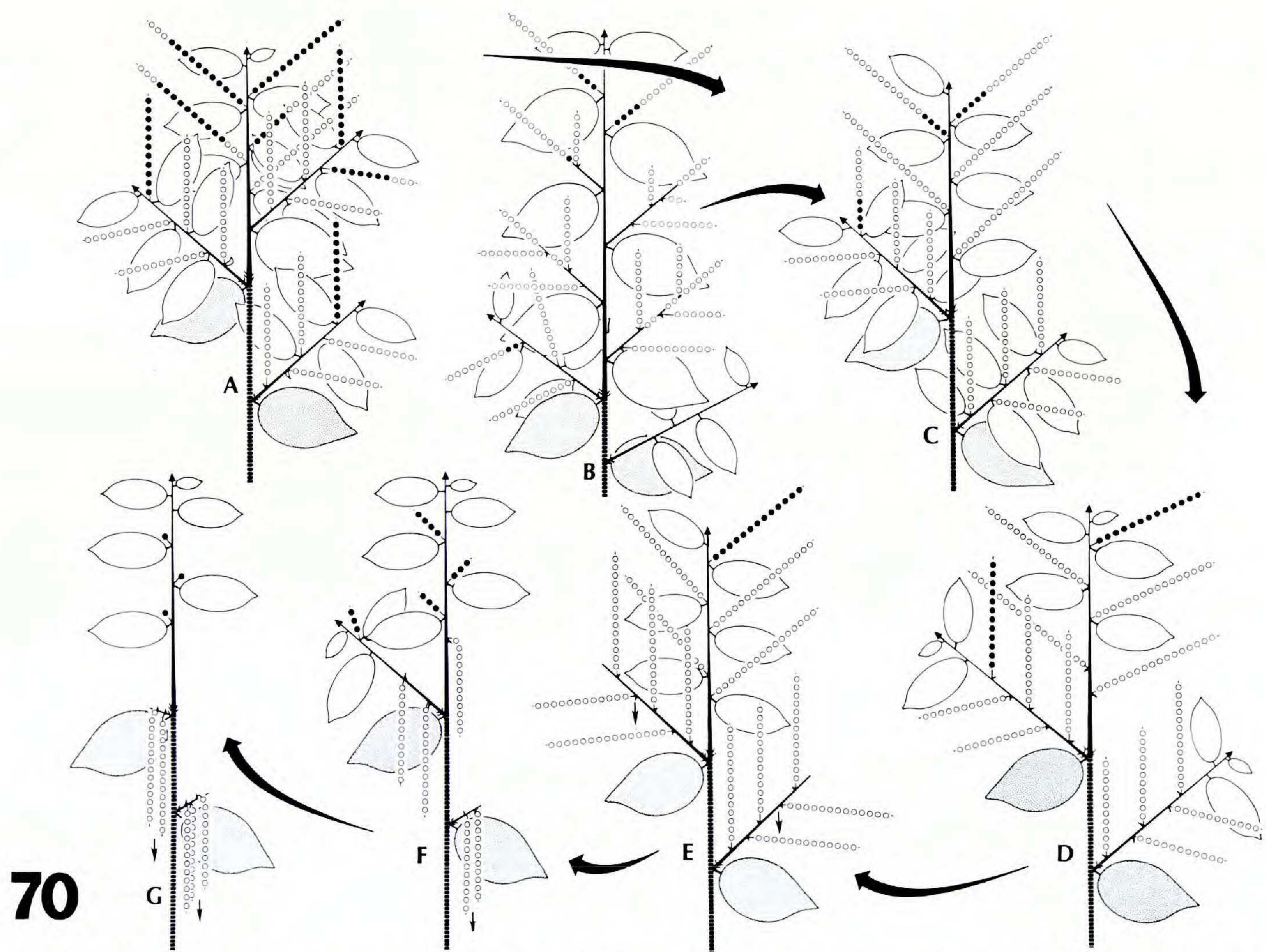


FIGURE 70. Possible derivations of inflorescence patterns in *Lithocarpus*, *Castanopsis*, *Castanea*, and *Quercus* (downward-pointing arrows indicate deciduous branches).

angiosperms, and that it was often reduced or lost in woody plants as they colonized cooler climates.

FIGURE 70 summarizes logical levels of specialization, based upon the concepts advanced above, in modern species of *Castanea*, *Castanopsis*, *Lithocarpus*, and *Quercus*. No hypothetical or extrafamilial patterns are shown. The coexistence of ancestral and derived characters among living members of such a large family is to be expected, although even the least derived stages (FIGURE 70A, B) are quite specialized for angiosperms. All the stages shown, as well as numerous intermediates and variants, are common in living Fagaceae and must be considered evolutionarily successful.

FIGURE 70A, B shows flowers of both sexes on some or all branches as well as on the leader—distributions common in *Lithocarpus* and *Castanopsis*. Some perfect flowers occur but are not indicated. Both illustrations also show proleptic and sylleptic indeterminate branches. The sylleptically branched staminate spikes of FIGURE 70B have perhaps preceded the condition in FIGURE 70C, where sylleptic branching is lost in both the leader and the spikes, and fertile branches are indeterminate with at least some exclusively staminate. Spikes are seldom ramified, and pistillate flowers are distal on the shoots but proximal on the spikes. This pattern occurs in *Castanea* (FIGURES 40–43) and some species of *Castanopsis*.

FIGURE 70D is similar to 70C, but the fertile portions of the branches are bracteose rather than foliose. Extension growth produces normal foliose leaves. The spikes are all unisexual. This pattern occurs in *Lithocarpus* (FIGURE 28) and *Castanopsis* (FIGURE 35).

In FIGURE 70E the branches are all proleptic and staminate. The upper branches are indeterminate, and the fertile region is bracteose. Lower branches are determinate and usually caducous. This combination of fertile determinate and indeterminate branches occurs in *Castanopsis* and *Lithocarpus*.

A common condition in Paleotropical *Quercus* is shown in FIGURE 70F. The leader has mostly pistillate spikes, and it sometimes has a few staminate catkins as well. Indeterminate branches can bear pistillate spikes and often have staminate catkins toward the base. Short-shoots bearing catkins are borne in leaf axils and are soon abscised.

The most extreme condition in extant Fagaceae is shown in FIGURE 70G and is commonest in northern *Quercus*. The pistillate spikes have one or few flowers. The leader lacks staminate catkins or has only a very few. The proximal branches are determinate, caducous short-shoots, and the distal branches are indeterminate. There are many variants of this and the preceding pattern.

The verticillate phyllotaxy and resultant verticillate display of inflorescences in *Trigonobalanus verticillata* is unique in the family, although some *Quercus* species produce crowded and essentially verticillate leaves near the end of a flush. Furthermore, *T. verticillata* produces alternate and then opposite leaves on many branches before forming whorled leaves with axillary inflorescences.

Forman (1964) believed the pendent catkins of *Quercus* and *Trigonobalanus daichangensis* to be derived from erect spikes of entomophilous Fagaceae, an opinion shared here and consistent with that of Schottky (1912). Forman (1964) also interpreted the single flowers on spikes and catkins of some *Quercus* and

TABLE 1. Probable evolutionary trends in fagaceous inflorescences.

CHARACTER	ANCESTRAL CONDITION	DERIVED CONDITION
1. Vegetative branching	sylleptic and proleptic	proleptic only
2. Branches	indeterminate, foliose	determinate, bracteose
3. Spike- and catkin-bearing branches	persistent	caducous
4. Flowers of spike-bearing branches	staminate and pistillate	staminate or pistillate
5. Flowers of leader	staminate and pistillate	pistillate only
6. Spikes	sylleptically branched	unbranched
7. Flowers of spikes	staminate and pistillate or perfect	staminate or pistillate
8. Staminate flowers borne in	spikes	catkins
9. Pistillate flowers on spikes	numerous	few or one
10. Pistillate flowers in total inflorescence	numerous	few to none

Trigonobalanus species as having been derived from dichasial clusters. *Trigonobalanus verticillata* and *T. excelsa* have dichasial flower clusters, while *T. daichangensis* has both clusters and single flowers. In addition, *T. daichangensis* has pendent catkins and is anemophilous, but the other two species have more or less erect male spikes and are probably entomophilous. Thus, *Trigonobalanus* is transitional between the entomophily of the Castaneoideae and the anemophily of *Quercus*.

Evolutionary increase in flower numbers is likely in some cases, especially in *Lithocarpus*, *Castanea*, and *Castanopsis*. On the other hand, there are fewer female flowers per spike and per total inflorescence in many northern Fagaceae. Catkins and spikes of *Quercus* generally bear fewer flowers than comparable axes of the other genera studied. Furthermore, there are reductions in floral and dichasial morphology in *Quercus*. The catkin can be interpreted as the least expensive structure, in terms of energy and materials, that can be produced quickly at the start of the relatively short temperate growing season. In addition, *Quercus* species in northern forests are conspecifically more gregarious and usually have fewer congeners than do species of *Lithocarpus*, *Castanopsis*, and *Quercus* in the tropics. In the north *Quercus* shows strong local conspecific pollination synchrony, while tropical *Lithocarpus* and *Castanopsis* (and perhaps *Quercus*, too) conspecifics frequently show marked reproductive asynchrony. The likelihood of successful pollination is thus perhaps as great in northern *Quercus* as in the other genera, which have more numerous flowers and are usually scattered in species-rich populations. The presence of relatively few species of *Quercus* in the lowland Paleotropics suggests that members of the genus have not been especially successful in migrating to warmer from cooler regions, where they probably originated. The converse is probably the case

with *Lithocarpus* and *Castanopsis*, both of which have fewer temperate than tropical species.

TABLE 1 summarizes likely evolutionary trends in fagaceous inflorescences, as portrayed in FIGURE 70. Intermediates and combinations of these characters can be found in many species and sometimes on a single individual. Within flower and fruit characters, ecology, and geography, there are correlates to these inflorescence characters but our data are as yet inconclusive. We suspect that inflorescence characters and fruit size are related. The range in dry-fruit weight in our Paleotropical specimens is from less than 0.5 to more than 60 g.

A few extant Fagaceae bear pedunculate pistillate cymules (e.g., FIGURES 1, 6, 8) that are perhaps indicative of ancestral thyrselike conditions. Soepadmo (1972) considered *Lithocarpus elegans* (Blume) Hatus. ex Soep. to be probably the most primitive in its genus. It has staminate cymules with up to 24 flowers, and pistillate ones with up to 10; the staminate spikes are frequently much branched. Hjelmqvist (1948) regarded *Lithocarpus* as the primitive genus in the family based on characters of the flowers and cymules. Our observations of inflorescences support that conclusion.

The Betulaceae are sometimes cited as the closest living relatives of the Fagaceae. Abbe (1935) showed the possible derivation of betulaceous inflorescences from thyrselike predecessors, a pattern perhaps similar to that of the Fagaceae. Jäger (1980) analyzed betulaceous inflorescences and postulated reduction in number and size of catkins, increase in winter protection of catkins, and reduction of leaf size, all associated with adaptation to colder climates with shorter growing seasons. The more primitive Betulaceae occur in warmer Sino-Himalayan areas. These attributes parallel those of the Fagaceae to some extent, but the Betulaceae are generally more northern and lack large numbers of tropical or subtropical species that might be of value for comparison. Further, there are no entomophilous Betulaceae.

Many inflorescence characters of the Fagaceae parallel those found by Manning (1938) in the Juglandaceae. That family exhibits trends 4–10 shown in TABLE 1. There are also geographic correlations of structure that point strongly to congruent biogeographic histories of the two families.

Čelakovský (1889) analyzed inflorescence patterns in the Fagaceae, Betulaceae, and Juglandaceae and found strong tendencies for proleptic shoots to be reproductive and bear reduced leaves. He interpreted single perfect flowers in leaf axils as primitive in these families' ancestors. In our study we have applied the principles of differentiation used by Čelakovský, with some modifications. We believe that he was correct in his assessment of fagaceous inflorescences, although his conclusions were based on only a few species. Further, we agree that the single perfect axillary flower is the primitive condition for angiosperms. The flower as a reproductive short-shoot is but one of a series of evolutionary repetitions of the tendencies to concentrate and elaborate reproductive structures.

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APPENDIX. Species studied and provenance of specimens.

CASTANEA

<i>C. crenata</i> Sieb. & Zucc.	Taiwan (cultivated)
<i>C. dentata</i> Borkh.	Nebraska (cultivated)
<i>C. mollissima</i> Blume	Nebraska (cultivated)

CASTANOPSIS

<i>C. acuminatissima</i> (Blume) A. DC.	Vietnam
<i>C. argyrophylla</i> King	Thailand
<i>C. armata</i> Spach	Thailand
<i>C. brevispina</i> Hayata	Taiwan
<i>C. chevalieri</i> Hickel & A. Camus	Vietnam
<i>C. chrysophylla</i> (Douglas) A. DC.	California, Oregon
<i>C. costata</i> (Blume) A. DC.	Borneo (Sabah)
<i>C. cuspidata</i> Schottky	Japan
<i>C. echinocarpa</i> A. DC.	Thailand
<i>C. ferox</i> Spach	Thailand
<i>C. fissa</i> (Champ.) Rehder & Wilson	Hong Kong
<i>C. formosana</i> (Skan) Hayata	Taiwan
<i>C. foxworthyi</i> Schottky	Borneo (Sabah)
<i>C. inermis</i> (Lindley) Bentham & Hooker f.	Malaya
<i>C. javanica</i> (Blume) A. DC.	Indonesia (Java)
<i>C. lanciifolia</i> (Roxb.) Hickel & A. Camus	Thailand

<i>C. longipetiolata</i> Hickel & A. Camus	Cambodia
<i>C. megacarpa</i> Gamble	Malaya
<i>C. motleyana</i> King	Borneo (Sarawak)
<i>C. nephelioides</i> King ex Hooker f.	Malaya
<i>C. philippinensis</i> (Blanco) Vidal	Philippines
<i>C. cf. pierrei</i> Hance	Thailand
<i>C. pyriformis</i> Hickel & A. Camus	Vietnam
<i>C. purpurea</i> Barnett	Thailand
<i>C. rhamnifolia</i> (Miq.) A. DC.	Thailand
<i>C. schefferiana</i> Hance	Malaya
<i>C. stellatospina</i> Hayata	Taiwan
<i>C. stipitata</i> Hayata	Taiwan
<i>C. subacuminata</i> Hayata	Taiwan
<i>C. tribuloides</i> (Smith) A. DC.	Burma
<i>C. tungurrut</i> (Blume) A. DC.	Indonesia (Java)

LITHOCARPUS

<i>L. aggregata</i> Barnett	Thailand
<i>L. amygdalifolia</i> (Skan) Hayata	Taiwan
<i>L. bennettii</i> (Miq.) Rehder	Borneo (Sabah)
<i>L. bolovenssis</i> A. Camus	Cambodia
<i>L. brevicaudata</i> Hayata	Taiwan
<i>L. buddii</i> (Merr.) A. Camus	Philippines
<i>L. cantleyana</i> (King) Rehder	Singapore
<i>L. caudatifolia</i> (Merr.) Rehder	Borneo (Sabah), Philippines
<i>L. celebica</i> (Miq.) Rehder	Philippines
<i>L. clementiana</i> (King ex Hooker f.) A. Camus	Borneo (Sarawak)
<i>L. conocarpa</i> (Oudem.) Rehder	Singapore
<i>L. cooperta</i> (Blanco) Rehder	Philippines
<i>L. cornea</i> (Lour.) Rehder	Hong Kong
<i>L. curtisii</i> (King ex Hooker f.) A. Camus	Malaya
<i>L. dasystachya</i> (Miq.) Rehder	Borneo (Sabah, Sarawak)
<i>L. dealbata</i> (Hooker f. & Thomson) Rehder	Burma, Thailand
<i>L. densiflora</i> (Hooker & Arn.) Rehder	California, Oregon
<i>L. echinocarpa</i> A. Camus	Vietnam
<i>L. edulis</i> Nakai	Japan
<i>L. elegans</i> (Blume) Hatus. ex Soep.	Thailand
<i>L. ewyckii</i> (Korth.) Rehder	Borneo (Sabah)
<i>L. fenestrata</i> (Roxb.) Rehder	Burma
<i>L. formosana</i> Hayata	Taiwan
<i>L. garrettiana</i> (Craib) A. Camus	Thailand
<i>L. gracilis</i> (Korth.) Soep.	Borneo (Sabah)
<i>L. hancei</i> (Bentham) Rehder	Hong Kong
<i>L. harmandii</i> (Hickel & A. Camus) A. Camus	Cambodia
<i>L. havilandii</i> (Stapf) Barnett	Borneo (Sabah)
<i>L. hendersoniana</i> A. Camus	Malaya
<i>L. hystrix</i> (Korth.) Rehder	Malaya
<i>L. kawakamii</i> Hayata	Taiwan
<i>L. kodaihoensis</i> Hayata	Taiwan
<i>L. konishii</i> (Hayata) Hayata	Taiwan
<i>L. lampadaria</i> (Gamble) A. Camus	Malaya
<i>L. leptogyne</i> (Korth.) Soep.	Borneo (Sarawak)
<i>L. lucida</i> (Roxb.) Rehder	Malaya
<i>L. macphailii</i> (M. R. Henderson) Barnett	Malaya
<i>L. maingayi</i> (Bentham) Rehder	Malaya

<i>L. meijeri</i> Soep.	Borneo (Sabah)
<i>L. mindanaënsis</i> (Elmer) Rehder	Philippines
<i>L. nantoensis</i> Koidz.	Taiwan
<i>L. neorobinsonii</i> A. Camus	Malaya
<i>L. nieuwenhuisii</i> (Seemen) A. Camus	Borneo (Sabah)
<i>L. nodosa</i> Soep.	Borneo (Sabah)
<i>L. papillifer</i> Hatus. ex Soep.	Borneo (Sabah)
<i>L. pattaniensis</i> Barnett	Malaya
<i>L. polystachya</i> (Wallich) Rehder	Thailand
<i>L. rassa</i> (Miq.) Rehder	Malaya
<i>L. reinwardtii</i> A. Camus	Cambodia
<i>L. rhombocarpa</i> Hayata	Taiwan
<i>L. rufovillosa</i> Soep.	New Guinea
<i>L. soleriana</i> (Vidal) Rehder	Philippines
<i>L. sootepensis</i> (Craib) A. Camus	Thailand
<i>L. sundaica</i> (Blume) Rehder	Borneo (Sarawak)
<i>L. ternaticupula</i> Hayata	Taiwan
<i>L. thomsonii</i> (Miq.) Rehder	Thailand
<i>L. truncata</i> (King ex Hooker f.) Rehder & Wilson	Burma
<i>L. turbinata</i> (Stapf) Forman	Borneo (Sabah)
<i>L. urceolaris</i> (Jack) Merr.	Borneo (Sabah)
<i>L. wallichiana</i> (Lindley ex Hance) Rehder	Malaya
<i>L. woodii</i> (Hance) A. Camus	Philippines
<i>L. wrayi</i> (King) A. Camus	Thailand

QUERCUS

<i>Q. acuta</i> Thunb.	Japan
<i>Q. borealis</i> Michaux	Nebraska
<i>Q. brandisiana</i> Kurz	Burma, Thailand
<i>Q. cambodiensis</i> Hickel & A. Camus	Cambodia
<i>Q. championii</i> Bentham	Hong Kong
<i>Q. chrysolepis</i> Liebm.	Oregon
<i>Q. elmeri</i> Merr.	Borneo (Sabah)
<i>Q. gilva</i> Blume	Japan, Taiwan
<i>Q. glauca</i> Thunb.	Taiwan
<i>Q. griffithii</i> Hooker f. & Thomson	Thailand
<i>Q. imbricaria</i> Michaux	Iowa
<i>Q. kinabaluensis</i> Soep.	Borneo (Sabah)
<i>Q. kingiana</i> Craib	Burma
<i>Q. lanata</i> Smith	Vietnam
<i>Q. lowii</i> King	Borneo (Sabah)
<i>Q. merrillii</i> Seemen	Borneo (Sarawak)
<i>Q. mespilifolioides</i> A. Camus	Thailand
<i>Q. morii</i> Hayata	Taiwan
<i>Q. myrsinaefolia</i> Blume	Japan
<i>Q. pachyloma</i> Seemen	Taiwan
<i>Q. paucidentata</i> Franchet	Japan
<i>Q. phillyraeoides</i> A. Gray	Taiwan
<i>Q. salicina</i> Blume	Japan
<i>Q. serrata</i> Thunb.	Japan, Thailand
<i>Q. stenophylloides</i> Hayata	Taiwan
<i>Q. subsericea</i> A. Camus	Borneo (Sabah)
<i>Q. uraiana</i> Hayata	Taiwan
<i>Q. valdinervosa</i> Soep.	Borneo (Sabah)
<i>Q. virginiana</i> Miller	Florida

TRIGONOBALANUS
T. verticillata Forman

Borneo (Sabah)

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